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# The Canadian Entomologist

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# The Canadian Entomologist

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# The Canadian Entomologist

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## The Effect of Weather and the Physical Attributes of White Pine Leaders on the Behaviour and Survival of the White Pine Weevil, *Pissodes strobi* Peck, in Mixed Stands[1]

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### Introduction

Over a century ago Peck (4) observed that open-growing stands of white pine, *Pinus strobus* L., were subjected to greater weevil damage than were those growing in mixture with, and shaded by, other tree species. This observation, which was later corroborated by Graham (2) and MacAloney (3), suggested possibilities of silvicultural control of the insect by means of plantation growing of white pine in various kinds of mixtures. The results of this work were recently assessed in a review paper by Belyea and Sullivan (1), who concluded that further silvicultural control measures be curtailed until the physical and biological requirements of the insect were defined in terms of measurable factors of the environment. Investigations were carried out (6, 7) to establish the conditions of temperature, light, and moisture favourable for feeding, copulation, and oviposition of the adults, and development of the larvae. The results indicated that *P. strobi* is well adjusted to the environmental conditions in open stands of white pine, but that the limitations imposed by weather on weevil oviposition might be a major factor contributing to the inability of the insect to adapt readily to the climate of many shaded stands. The present paper is an attempt to assess the role of weather and the physical characteristics of white pine leaders, hereafter called leaders, in limiting the successful invasion, by the weevil, of white pine stands growing as partially suppressed, understory trees. Emphasis is placed on providing an understanding of the differences in the climate of weevil habitats, adult feeding and oviposition behaviour, and survival of weevil populations in exposed and shaded stands of white pine. In addition, records were obtained for the purpose of forecasting differences in both the timing and amount of such acts as oviposition and feeding in populations in the two habitats.

The investigation was carried out in exposed and shaded stands of white pine characterizing extreme conditions from the standpoint of weevil abundance. The study areas were situated in the Petawawa Forest Experiment Station, Chalk River, Ontario, and the Bonnechere Valley Management Unit, in the Pembroke District of the Ontario Department of Lands and Forests. Areas were selected on the basis of uniformity of forest stands, overstory species, and amount of weevilling of the white pine. On occasion, it was necessary to introduce weevils into the shaded stand to obtain data on their behaviour, habits, and survival.

### Feeding and Oviposition Behaviour in Exposed and Shaded Stands as Affected by the Microenvironment and Leader Characteristics

#### *Feeding and Oviposition Behaviour*

In open-growing stands during spring, feeding and oviposition punctures are first made by *P. strobi* adults in the leader just below the buds and occasionally in the buds themselves. The insects confine their attack to the leading shoot of

[1]Contribution No. 712, Forest Biology Division, Department of Forestry, Ottawa, Canada; a portion of this paper is based on part of a thesis submitted as partial fulfilment for the degree of Doctor of Philosophy at Macdonald College, McGill University, 1957.

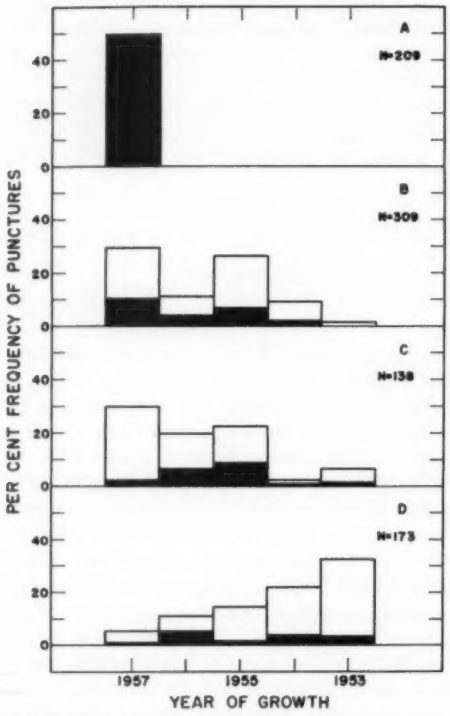


Fig. 1. Percentage frequency of oviposition punctures (shaded areas) superimposed over the percentage frequency of feeding punctures of *P. strobi* adults at the end of the 1958 season of activity. A, exposed leader in a heavily infested stand; B, C, D, shaded leaders in a stand where weevil damage is negligible.

the previous year and as more and more punctures appear in the upper portion of it, the weevils move farther down so that, by the end of the season, the distribution of punctures is relatively even throughout the length of the leader. The progressive development of this behaviour pattern during the oviposition period has been followed in the field. The results indicate that whereas feeding constitutes the main activity during the early portion of the active season of the adults, oviposition increases in intensity until an almost equal number of empty punctures and punctures containing eggs are observed by the end of the season of activity (Fig. 1A). There is, however, a tendency to a greater proportion of oviposition punctures near the leader tip. Although this is not of consequence in the overall distribution of feeding and oviposition punctures, which remain remarkably similar, it indicates that the insect continually returns to the leader tip, following inactive periods or movements to new trees, before beginning to search for a suitable feeding and oviposition site—a basic characteristic of weevil behaviour.

On shaded trees the pattern of distribution and frequency of feeding and oviposition punctures differed greatly from that observed in exposed sites. These observations were made in a young stand of white pine shaded by a canopy of red oak, *Quercus rubra* L. Weevil adults were placed on 17 understory white pine leaders in screen cages enclosing the leader and at least four years of earlier growth. Five male and five female weevils were introduced into each cage. In Fig. 1, a

TABLE I

Incidence of oviposition by *P. strobi* adults in shaded white pine attacked in 1958.

| Tree No. | Years of growth attacked | Diam. range of attacked growth (mm.) | Total no. of punctures | % punctures containing eggs |
|---|---|---|---|---|
| 1 | 1957–1953 | 3.5–10.4 | 138 | 19.6 |
| 2 | 1957–1953 | 2.6– 8.9 | 173 | 15.0 |
| 3 | 1957–1953 | 3.0–10.1 | 309 | 23.0 |
| 4 | 1957–1955 | 5.0–11.7 | 69 | 27.5 |
| 5 | 1957–1954 | 3.8–11.8 | 105 | 15.2 |

comparison is made of the behaviour of the adult when presented with shaded leaders in this stand (Fig. IB, C, D) and when presented with an exposed leader in the other stand (Fig. IA).

On the shaded stems the attack is not confined to the terminal shoot as it is on the exposed or control tree; it occurs over the main stem of the past four or five years growth. In addition, there is no indication of equal numbers of feeding and oviposition punctures, nor any regularity in relation to position on the main stem. Table I records the number of punctures made by the insects in five of the enclosed stems and the percentage of these that contained eggs. Fig. 2 illustrates the typical distribution pattern of the punctures on each of five one-year growths on the main stem at one of the shaded stations. In this case, the attack in 1958 extended over the terminal growth of 1957 to 1953, inclusive. A total of 173 punctures were made during the season, of which only 26, or 15 per cent, contained eggs.

There was no significant correlation between changes in microenvironmental conditions along shaded stems and the distribution of the punctures over four or five years growth of a main stem. Temperatures of the bark surface recorded over the area of attack were practically identical; from the upper to the lower levels of attack, the differences were of the order of 0 to 1.5° C. Additional observations indicated that the presence of the screens did not promote a greenhouse effect about the enclosed stems.

One obvious difference between trees on the exposed and shaded sites was that the shaded stems produced less vigorous and thinner leaders. Measurements showed that the average diameter of a sample of 122 leaders in the shaded site was 3.6 ± .07 mm., compared to 7.7 ± .13 mm., for a sample of 199 in the adjacent exposed site. To compensate for this general difference in leader quality between the two sites, six typical young white pines were transplanted from the exposed to the shaded site. Five of the stems were caged, one was left uncaged, and weevils were introduced in the manner earlier described. Examination of the stems following the oviposition period showed that weevil feeding and oviposition was almost entirely limited to the leaders. In general, more punctures were made than on the naturally occurring caged stems in the stand, but the percentage containing eggs was comparable. For example, critical examination of two of the caged stems, with upper diameters of 8.6 and 7.0 mm., showed that they contained 487 and 411 punctures, respectively, and that 19 and 28 per cent contained eggs.

*Microenvironment*

The foregoing results indicate differences in weevil behaviour in the two sites that affect population survival. For example, it has been shown that there

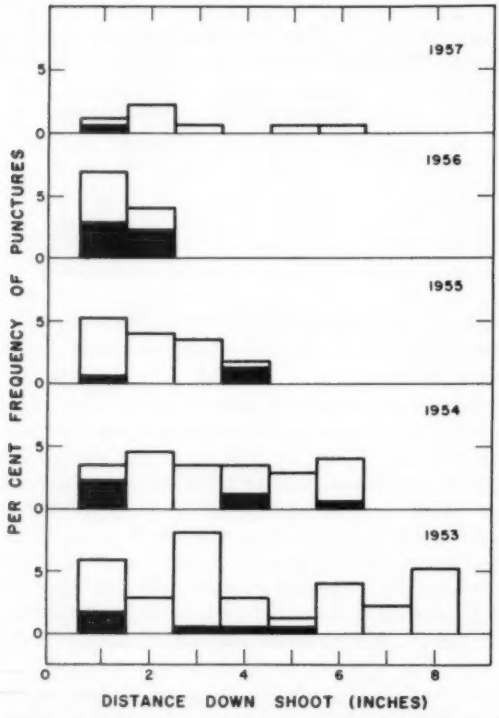


Fig. 2. Typical distribution pattern of 173 punctures made by *P. strobi* adults in 1958 on five years growth of the main stem of a shaded white pine. Shaded areas represent the percentage of the total number of punctures containing eggs superimposed over the percentage of the total number of punctures representing feeding outlets.

is a marked reduction in amount of weevil feeding and, particularly, oviposition in the shaded stand. The explanation for this may be found in the influence that the microenvironment of the habitat exerts on these activities. Comparative microenvironmental measurements were made primarily in a heavily weevilled, exposed stand of white pine and a mixed stand of hardwoods and white pine. The hardwood canopy was provided by about 480 stems per acre of *Populus tremuloides* (69%), *P. grandidentata* (24%), and *Betula papyrifera* (7%), averaging 5.0, 8.5, and 4.0 inches DBH, respectively. The white pine understory was lightly weevilled by a population of adults introduced the previous autumn, before the onset of hibernation. In the exposed stand, 64 per cent of the leaders showed adult damage and 45 per cent of the attacked stems died as a result of larval feeding. In the shaded, mixed stand, five per cent of the leaders exhibited evidence of light adult feeding and oviposition, but none died.

Observations on mortality of weevil adults during hibernation, and the rate of emergence from hibernation in the two stands were made on a total of 768 caged adults, divided into four equal groups and introduced into four overwintering cages, two in each plot. Mortality during hibernation amounted to 15 and 29 per cent in the exposed and shaded plots, respectively. Emergence from hibernation in the exposed stand spanned the period April 23 to May 12, and in the shaded stand, April 27 to May 13, but in both plots, peak emergence occurred

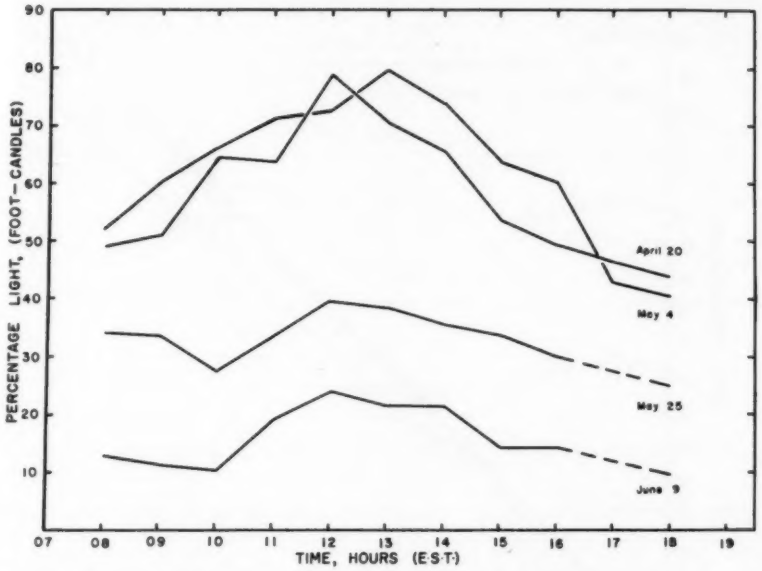


Fig. 3. Percentage of maximum light reaching white pine leaders under an aspen canopy, on four clear days during April, May, and June, 1959.

during the week of May 1-7. First oviposition occurred on April 30 at the open site and May 3 at the shaded site.

One of the main objectives in this study was to obtain comparable data from the stands over a period of several weeks. This has been discussed by Wellington (10), who proposed collecting pertinent data during days on which preselected types of weather occur. In this particular study, the "type" days selected corresponded with the periods having the greatest significance to the insect. Thus, intensive studies involving the measurement of light penetration into the stands and the microclimate of weevil habitats were confined to the clear, warm, relatively dry days during spring that are associated with the passage of modified arctic continental air over the station and during which weevil activity is maintained at a high level. Continuous weather records were obtained through the use of standard Stevenson screen equipment and a microbarograph, and hourly cloud, wind, and rain observations.

Light penetration, measured with a Weston Model 756 illumination meter, was used as the standard of comparison for stands of different densities. Readings at leader height were obtained at hourly intervals from ten or more stations along a line strung through the shaded stand, and compared with simultaneous readings taken in fully exposed sites. Fig. 3 shows the percentage of maximum available light that reached the leaders under the aspen canopy on four clear days that occurred at intervals during the period extending from about two weeks before to the end of the growth of the foliage canopy (April 20 to June 9). With increasing solar elevation, there was a gradual increase in light penetration until the aspen leaves opened on May 3. Throughout the remainder of the season, the per cent penetration decreased progressively in conjunction with the development

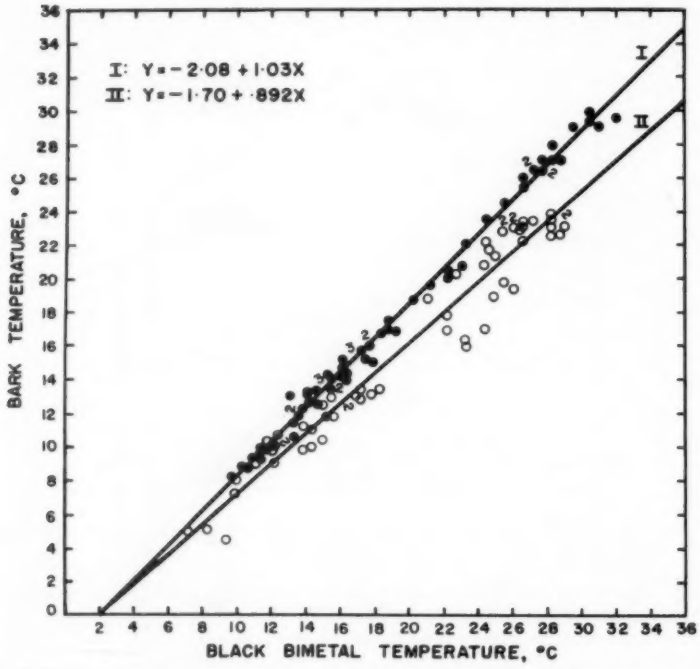


Fig. 4. Clear day relation between white pine leader bark temperature and black bimetal temperature. I: open site; II: shaded site.

of the hardwood canopy. At all times of the season, however, the greatest penetration occurred around midday, when the sun was near its maximum elevation.

Corresponding with the changing light conditions throughout the season, marked changes occurred in the temperature of weevil feeding and oviposition sites. Temperature measurements were obtained as follows: thermocouples recording on a portable potentiometer were used to establish the relationship between bark tempreature of the leader (the temperature exerting the greatest effect on weevil activity (Sullivan, 7)), and thermographs with exposed black bimetal sensing elements (cf. Wellington (9)). Temperatures as measured by such thermographs are closely related to actual bark temperatures of the leaders (Fig.4), and they greatly facilitate such measurements. From Fig. 4, it is obvious that the relationships between actual bark temperatures and thermograph temperatures are different in the exposed and shaded sites, the relationship being much closer in the exposed site. This is due to the irregular penetration of solar radiation into the shaded stand, and the lag in response of the thermograph. Since the differences are regular over the range of temperatures studied, these discrepancies present no real problem and thermograph records equated to bark temperatures are suitable for relating to weevil activity in both types of sites. Graphic representation of the temperature variations at the two sites is shown in Fig. 5, which illustrates the daily trend of the temperature of the bark of leaders and the air temperature at the exposed and shaded stations at three periods of the season. Nominal differences in air temperature occurred between the two sites, the general trend being to slightly cooler nocturnal and warmer diurnal conditions at the exposed

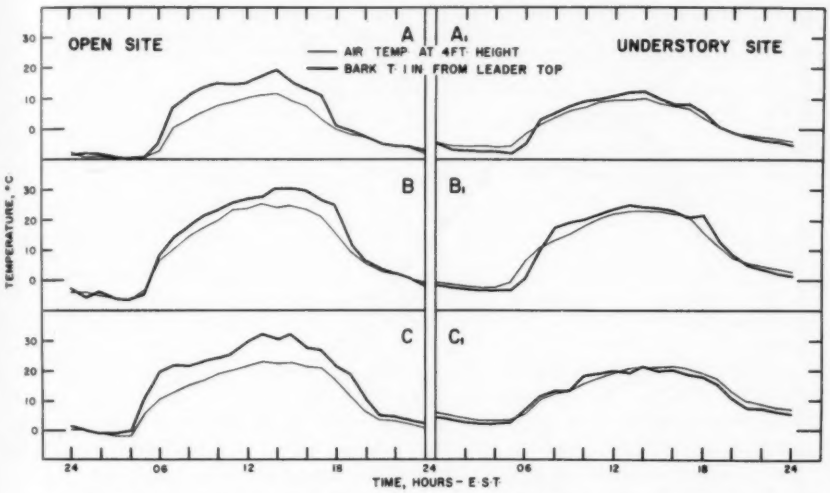


Fig. 5. Air temperatures and bark temperatures of white pine leaders at open and understory sites. $A,A_1$, April 20; $B,B_1$, May 3; $C,C_1$, June 2, 1959.

site. A similar trend in bark temperature was observed, but during the diurnal period, a considerable difference occurred between the two sites, in accordance with a change in the radiant heating effects of the sun proportional to the amount of shade. At the open site, diurnal bark temperatures were continually maintained above the air temperature throughout the season. Similarly, at the shaded site during the early part of the season (Fig. $5A_1$, $B_1$), insolation was sufficient to maintain the bark temperature of weevil habitats above the air temperature throughout most of the diurnal period, although the difference between the two was not as great as that at the open site. Later in the season, however, insolation was reduced to the point where shaded habitats had bark temperatures corresponding almost exactly with the daily air temperature regime (Fig. $5C_1$).

The interrelation of canopy development, insolation, and weevil habitat temperatures is shown in Fig. 6. Part of this figure shows the percentage growth curves of the overstory aspen foliage and the seasonal trend of light penetration to the white pine understory. It is apparent that insolation is reduced in proportion to the amount of growth of the foliage canopy. Superimposed over these curves is the seasonal trend of temperature differences between the bark of the shaded and exposed leaders, recorded on relatively clear, calm days, during the period extending from mid-April to late June. The bark temperatures were obtained by averaging black bimetal temperatures recorded at 0900, 1300, and 1700 hours, and correcting them to the bark temperature level as shown in Fig. 4. Fig. 6 shows that at no time during the season of weevil activity were the bark temperatures of exposed and shaded leaders equal. During the period April 20 to May 3, the bark temperatures of the shaded leaders ranged from approximately 8 to 3°C, respectively, below comparable sites in the open-growing stand. This general decrease in bark temperature differences between the two sites continued to the time the aspen leaves opened, and may be explained on the basis of changing solar elevation and radiant heating. Throughout the period May 3 to June 9, the amount of shade increased with corresponding reductions in insolation, so that

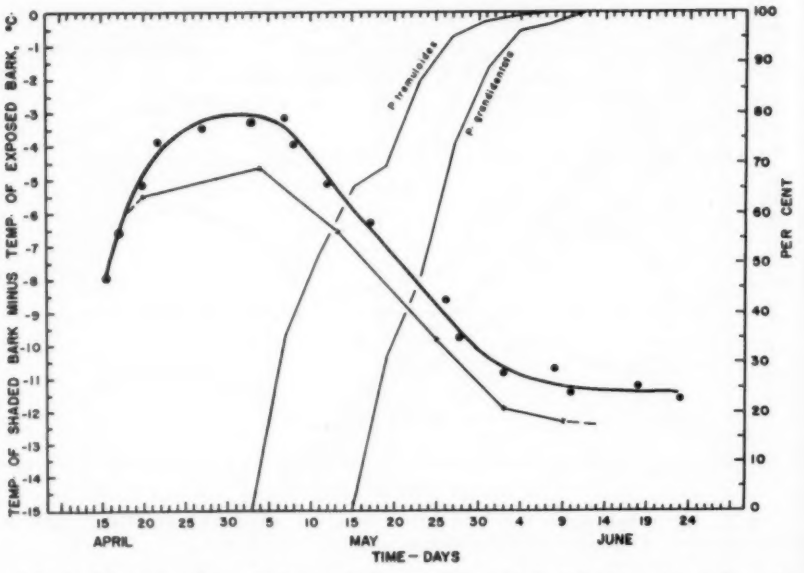


Fig. 6. The seasonal trend of mean bark temperature of shaded white pine leaders minus the mean bark temperature of exposed leaders superimposed over the per cent growth curves of aspen foliage and the seasonal trend of light penetration to understory white pine. Crosses: per cent light penetration; dots: temperature differences.

the bark temperatures of the shaded stems ranged from about 3 to 11°C, below comparable stems in the exposed stand.

An increase in atmospheric moisture was associated with the reduction in light and temperature in the shaded stand of pine. Measurements showed that, at the time *P. tremuloides* leaves began to open, the relative humidity in shade was 0 to 10 per cent above that in the open. With the development of the foliage canopy, the difference in humidity varied from about 5 to 30 per cent.

The above comparisons show that weevils located at the shaded site are subjected to a microenvironment maintained at levels below that of exposed habitats; the shaded site is characterized by cooler, moister conditions. The effect of this difference in regulating the amount of weevil activity may be shown by interpreting the microenvironments of weevil habitats at the two sites in terms of probable weevil feeding and oviposition. The limitations imposed on weevil activity by temperature and moisture, in their preferred, exposed habitats have been discussed in an earlier paper (7), and are used here as a basis for comparison. There it was shown that the percentage of a population engaged in these activities is regulated to a large extent by the temperature and moisture conditions of the habitat. These relations were expressed by activity isopleths drawn between axes of bark temperature and relative humidity. It was obvious that weevil feeding may be maintained at a relatively high level over a wide range of temperature and moisture, and that oviposition activity is confined to a very narrow range.

Two clear, calm days during which modified arctic air masses occupied the area have been selected to show the relationships. The first day corresponds with the time of first weevil oviposition in the shaded stand, during the period of minimum temperature differences between weevil habitats in the two sites; the

TABLE II

Maximum possible feeding and oviposition by a population of *P. strobi* adults at various combinations of leader bark temperature and relative humidity on clear days in an understory white pine stand, based on observed relationships in an open stand of white pine.

| | Per Cent Activity | |
|---|---|---|
| | Feeding | Oviposition |
| Early season (without foliage canopy) | 70 | 60 |
| Late season (with foliage canopy) | 55 | 20 |

second with the latter part of the active period of weevil oviposition, during the time of maximum temperature differences between weevil habitats at the two sites. The results (Table II) show that the maximum percentage of weevil feeding and oviposition that could occur varies throughout the season in accordance with changes in habitat microenvironment. It is also obvious that the critical period for weevil attack in a shaded stand is when the shade provided by the canopy is at a minimum. During this part of the season, however, the portion of the population that has reached the physiological state associated with oviposition represents only about one per cent of the adults that survive hibernation. Examination of the records indicates that first oviposition by 50 per cent or more of the population occurred between May 12 to 20. This period corresponds with the time that shading by the hardwood canopy reduced insolation by 45 to 60 per cent with resultant depressions in habitat temperatures of 5 to 8°C. below the temperatures of exposed sites. Oviposition activity during this period was reduced from about 55 to 35 per cent of that at exposed sites.

*Leader Characteristics*

The results described above indicate that the microenvironment of shaded habitats is responsible for a marked reduction in oviposition activity, but it is clear that it does not entirely eliminate it. Elimination is more likely when microenvironmental effects are combined with the effects of certain attributes of white pine leaders on weevil behaviour. The distribution pattern of the punctures on thin and thick stems indicates that the response mechanism of the insect is related to the physical vigour of the leader. Since leader vigour may be expressed in terms of length and diameter, a series of tests was conducted under insectary conditions, in which weevil adults were introduced into screened cages containing combinations of short, long, thick, and thin leaders. Following exposure to weevil attack for one week, the leaders were re-examined and the number of punctures used as the criterion of preference. Table III shows the preference for leaders of different length when the diameter is held constant, and for leaders of different diameter when the length is held constant. The high standard errors obtained were due mainly to an unavoidable variation in the number of adults contained in the cages during the tests. The results indicate, however, that weevil adults exhibit a definite preference for thick leaders irrespective of length.

In the field, 500 exposed leaders were tagged and measurements of their upper diameter obtained before growth initiation in the spring. Following the

TABLE III

Preference of *P. strobi* adults for white pine leaders of particular vigour.

| | Number of Punctures | | | |
|---|---|---|---|---|
| | Test 1 | | Test 2 | |
| | short thick | long thick | short thick | short thin |
| N | 12 | 12 | 8 | 8 |
| $\bar{X}$ | 63.9 | 65.8 | 100.2 | 38.2 |
| $S_{\bar{x}}$ | 9.576 | 12.210 | 12.104 | 10.267 |
| P | > .50 | | < .01 | |

N, sample size; $\bar{X}$, mean number of punctures per leader; $S_{\bar{x}}$, standard error of mean; P, probability.

season of adult attack, the leaders were re-examined and the extent of attack recorded. The results are shown in Fig. 7. Fig. 7A shows the incidence of leaders in one-millimetre upper diameter classes within the sample, and Fig. 7B shows the percentage of the leaders in each of the classes that were attacked by weevil adults. Leaders of 4 mm. diameter, or smaller, were rejected, but the amount of attack steadily increased in relation to increases in diameter to 9 mm., where about 80 per cent of the leaders were attacked. Although the incidence of leaders above 9 mm. diameter drops rapidly in the stand, the percentage of attack on those occurring in the 10 and 11 mm. diameter classes is maintained near 80 per cent. Despite the fact that, at higher diameters, there is some indication of a decrease in the percentage of leaders attacked, Fig. 7C shows that the level of attack to which the leaders were subjected, increased in relation to the increases in diameter.

The diameter classes most frequently attacked by the insect are rarely found in shaded stands. Measurements showed that in the shaded stand, the average leader diameter of the white pine was 3.9 ± .023 mm., and in the exposed plot, 9.3 ± .19 mm. When forced to remain on the thin stems, characteristic of the understory, the adults exhibit the pattern of feeding and oviposition behaviour shown in Fig. 1B, C, D. If, however, they are forced to remain on thick stems introduced into the shaded stand, the adults exhibit the pattern of oviposition and feeding behaviour shown in Fig. 1A, but fewer eggs are deposited. Finally, uncaged adults liberated in the shaded stand tend to leave the area, so that the naturally occurring understory pines are subjected to only a nominal amount of feeding and oviposition.

Although these results show that weevil oviposition and feeding is confined to leaders of particular "vigour", the basic question of why such leaders are preferred remains unanswered. Preliminary studies showed that variations in the incidence of needle clusters per unit area on thin and thick leaders is not a factor contributing to the selection. Additional observations, however, indicated that the thickness of the bark influences the selective reaction. In this respect, observations were made on the ratio of wood to bark thickness over a range of outer diameters, in an effort to determine if xylem thickness tended to be constant with outer diameter variations attributable to variations in phloem thickness. Thirty-two leaders, with upper diameters ranging from 3.1 to 12 mm., were

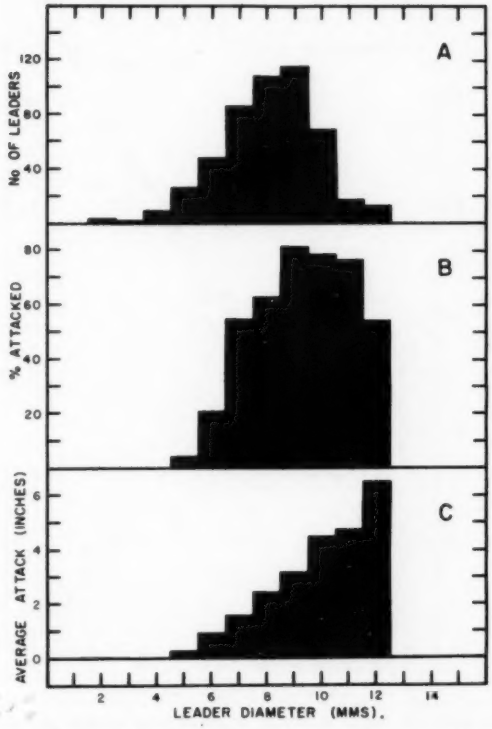


Fig. 7. Incidence of *P. strobi* adult attack on 500 open-grown white pine. A, frequency of leader diameter classes in the stand; B, relation between per cent of leaders attacked and leader diameter; C, relation between the amount of adult attack and leader diameter.

examined and it was apparent that the outer diameter variation could be attributed almost equally to changes in xylem thickness and phloem thickness. This held true not only for the upper part of the leader, but for the middle and lower portions as well. It was obvious, however, that the bark thickness of the leader was closely related to the outer diameter. This is illustrated in Fig. 8, which shows that increases in outer diameter measurements near the top of the leaders are accompanied by increases in bark thickness. Since there is simply a progressive increase in bark thickness within the limits of the range of leader diameters examined, no major difference in the relation between the thickness of the bark and leader diameter was observed above and below the minimum outer diameter level acceptable by the insect. Interpolation in Figs. 7B and 8 shows, however, that weevil adults have a preferred range of bark thickness on which to initiate feeding and oviposition. This range extends from 0.8 to 2.5 mm., with the greatest preference being shown for bark ranging in thickness from about 1.8 to 2.2 mm., a range not characteristic of the leaders at the shaded station. In addition, the average size of the oblong weevil egg, 0.8 by 0.5 mm., serves to delimit the lower level of the acceptable bark thickness range, simply because bark thinner than about 0.8 mm. would probably be unsuitable for the deposition of an egg.

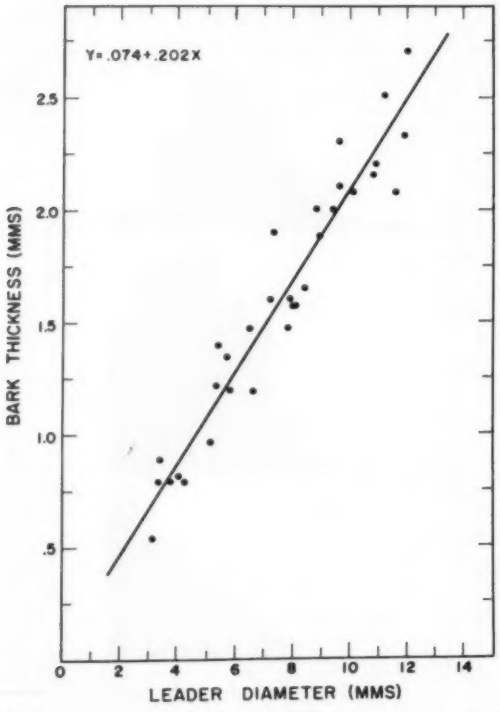


Fig. 8. Relation between upper diameter of white pine leaders and thickness of the bark at the same level on the leaders.

## Survival

The foregoing section shows that the success or failure of weevil invasions of partially suppressed understory white pine is determined by the oviposition and feeding behaviour of the adults and by the physical attributes of white pine leaders. The ultimate effect of these factors on the further development of the insect may be expressed through a consideration of the survival of the immature stages in the two habitats. The results discussed below refer only to weevil populations in white pine stands within the northern range of the insect, but the methods used might be very useful in determining the suitability of existing habitat conditions for weevil development throughout the entire range of the insect.

*Exposed Site*

Taylor (8) estimated that the percentage of eggs from one year represented by mating forms the following spring ranged from 2.5 to 5.0 per cent, based on an assumed average of 100 to 125 eggs per leader, actual larval counts, and assumed mortality during the autumn and winter. Although these figures may be useful for some purposes, they do not satisfactorily indicate the numerical stability of the population. One of the chief weaknesses in the work appears in the estimation of the number of eggs per leader. The number of eggs found on a leader may be related to the severity of adult attack as shown in Fig. 9, which embodies information from 81 white pine leaders, varying in upper diameter

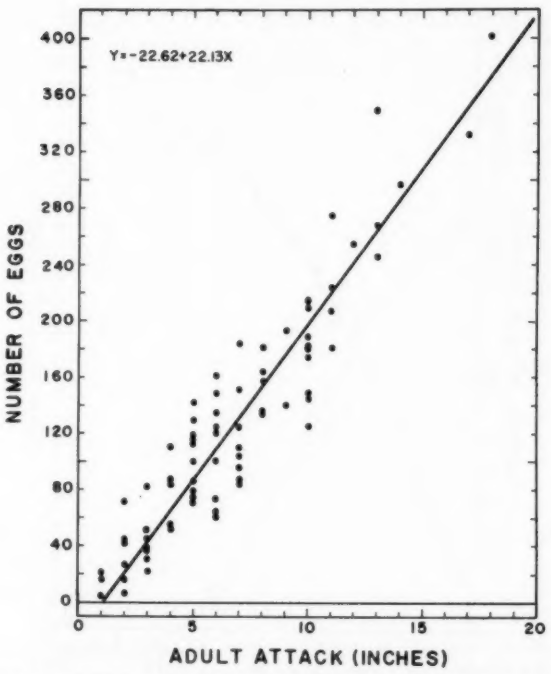


Fig. 9. Relation between amount of attack by *P. strobi* adults and number of eggs deposited.

from 6 to 10 mm. The correlation coefficient of 0.956 is significant beyond the 0.001 level. Approximately 90 per cent of the variance is accounted for through correlation with adult attack, and the remainder probably is ascribable to differences in the diameter of the leaders making up the sample.

The amount of larval damage is related to the severity of adult attack as shown in Fig. 10, where a second degree polynomial curve has been fitted to the data. By interpolation in Figs. 9 and 10, the relationship between the amount of larval damage and the number of eggs occurring on a leader may be determined. This relationship, as shown in Fig. 11, is curvilinear. The reduction in larval damage at higher egg densities is a reflection of competition between larvae for space and food.

The number of adults emerging from infested leaders is related to the severity of larval damage in Fig. 12, where a second degree polynomial has been fitted to the data. By interpolation in Figs. 11 and 12, the relation between the number of eggs present in a leader and the number of adults emerging may be determined. This relationship (Fig. 13A), which is curvilinear, shows the reduction in number of adults emerging at the higher egg densities – a further reflection of the competition between larvae for space and food.

Fig. 13B illustrates the relation between egg density and the percentage of eggs representing successful development to the adult stage. The highest percentage of eggs giving rise to adults occurs in leaders containing between 145 and 220 eggs; within this range, 3.0 to 3.1 per cent of the eggs are represented by

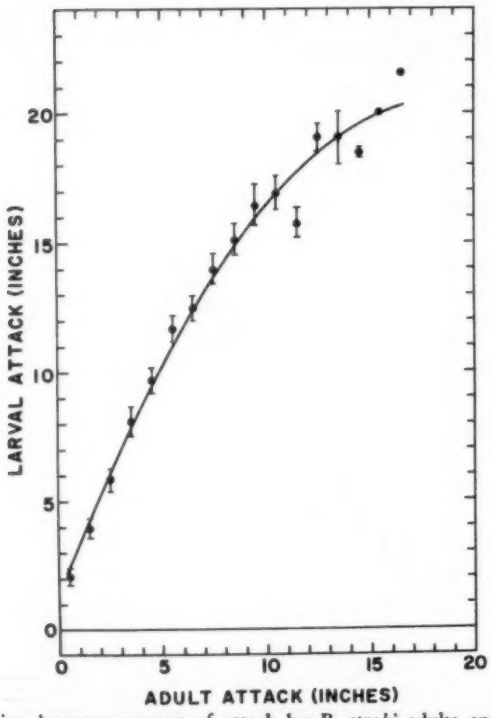


Fig. 10. Relation between amount of attack by *P. strobi* adults and amount of larval damage. The fine lines through the means represent one standard error.

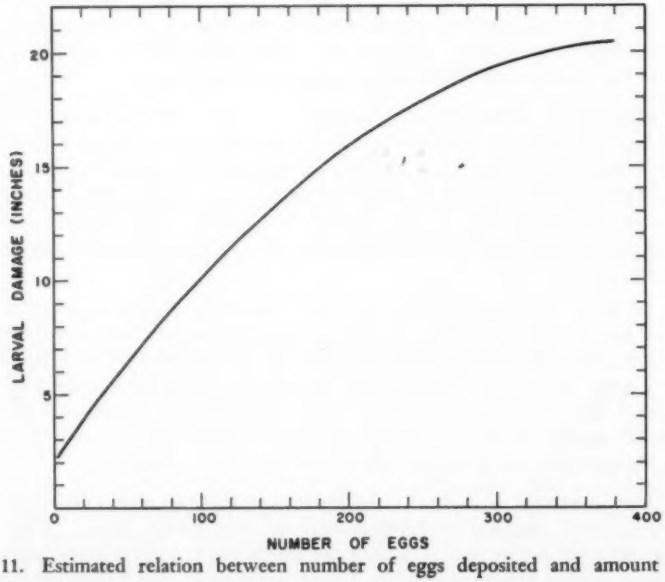


Fig. 11. Estimated relation between number of eggs deposited and amount of larval damage.

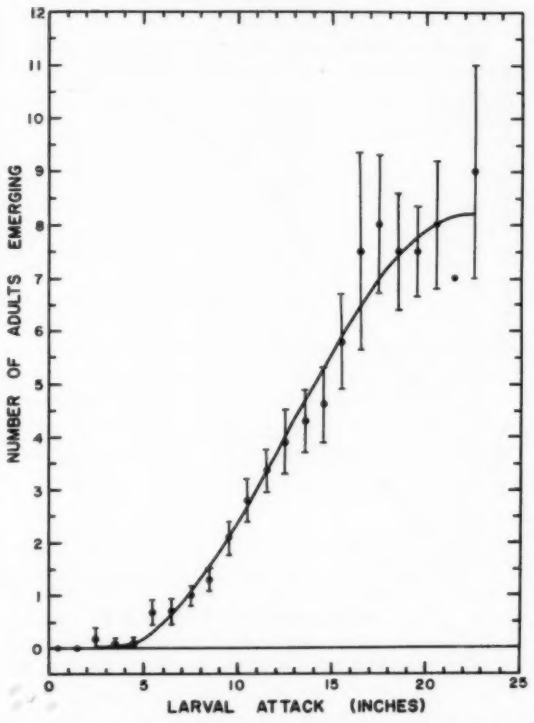


Fig. 12. Relation between *P. strobi* larval attack and number of adults emerging from the infested shoots. The fine lines through the means represent one standard error.

adults emerging. Of the entire egg complement in 418 leaders originally infested with larvae over a range of 1 to 23 inches of attack, about 2.6 per cent produced adults.

These results were checked during studies designed to determine mortality within each phase of weevil development. New samples of infested leaders had to be examined at appropriate times of the season, because the weevil spends all stages with the exception of the adult confined within the bark and xylem tissue, and further development was prevented by dissection of the leaders. Consequently, in determining larval mortality, the original number of eggs deposited in a sample of leaders was determined from Fig. 11 and by the per cent hatch from earlier observations on egg survival. In addition, examination of leaders from which a known number of adults had emerged allowed assessment of prior mortality. Additional studies revealed that adult mortality before the onset of hibernation amounted to about 17 per cent, and that 16 per cent died during hibernation.

Table IV shows the generation mortality, the values in column three being based on an average female egg complement of 125. The greatest mortality occurs during larval development. In terms of survival, the number of eggs of one generation, which are represented by adults emerging from hibernation the following spring, is about 2.3. Because the ratio of male to female weevils is about 1:1, it appears that the requisite conditions for a growing population in

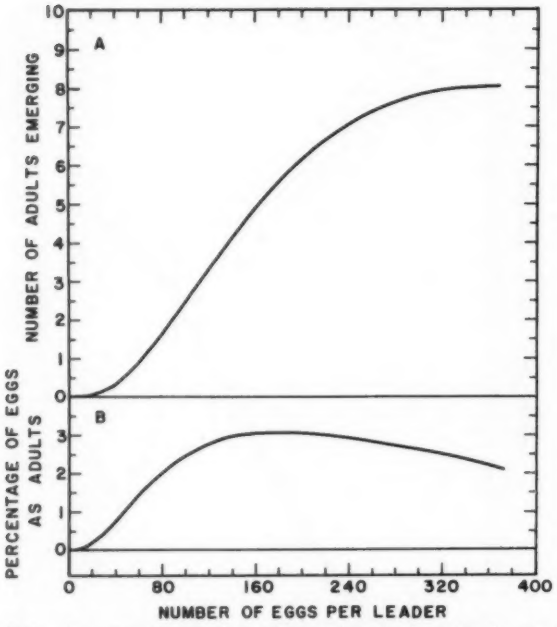


Fig. 13. Relation between the number of eggs deposited per leader by *P. strobi* adults and: A, number of adults emerging per leader; B, percentage of eggs represented by adults emerging per leader.

young, open-growing stands is realized through population survival. The small level of success, however, indicates that population growth is slow and that weevil populations are, numerically, quite stable.

*Shaded Site*

Unsuccessful attempts were made to establish weevil populations in understory pine stands during the spring and early summer. Untagged adults and adults labelled externally with radio-active cobalt were liberated in mixed stands. The results indicated that a greater amount of mortality occurred among adults in shaded than in open sites. In addition, many of the adults were lost and presumed to have left the area before sufficient damage had occurred to obtain satisfactory records of survival. Therefore, detailed observations were made only on caged stems in conjunction with the observations on weevil feeding and oviposition behaviour. Twelve naturally occurring, thin stems, with upper diameters ranging from 3.0 to 5.1 mm., and four of the introduced thick, vigorous stems, with upper diameters ranging from 7.4 to 8.9 mm., were available for observation.

The techniques employed in estimating weevil survival at the exposed site could not be used at the shaded site because of the failure of the adults to follow particular feeding and oviposition patterns. The oviposition punctures were distributed over four- or five-years growth of the main stem in a manner similar to that shown in Fig. 1. In addition, counts made on the number of feeding and oviposition punctures (Table I) showed that only a small number of eggs were deposited in each leader. Examination of the remaining 12 leaders showed that larvae, emerging from widely scattered eggs, generally fed individually rather

TABLE IV

Survival of *P. strobi* through one complete generation.

| Stage of development | Per Cent mortality | Survival of an ave. ♀ egg complement of 125 |
|---|---|---|
| egg | 6 | 117.5 |
| larva | 90 | 11.7 |
| prepupa | 68 | 3.7 |
| pupa | 5 | 3.5 |
| adult (before emergence) | 4 | 3.4 |
| adult (before hibernation) | 17 | 2.8 |
| adult (during hibernation) | 16 | 2.3 |

than in aggregations at a common feeding site. Aggregations occurred in only two leaders and, in both cases, the leaders and the current year's growth were killed. Four mature and four prepupal larvae were recovered from these stems, but all had died before completing development to adults. In the eight remaining leaders, individual larval trails ranged in length from about 0.1 to 4 inches. The larvae were encased in resin globules, indicating that pitch-drowning was a factor contributing to their death.

Among the three caged, stout-leadered stems, adult feeding and oviposition was confined primarily to the leading shoot. Larval damage was heavy and the terminal growth killed. The larvae survived long enough to form aggregations at a common feeding site, but none completed development to emerge as adults. The single uncaged stem suffered only light adult and larval damage, and the terminal growth survived. It is likely that the insects placed on this tree, being given a choice, left the stand entirely.

## Discussion

It has been pointed out that adults of the white pine weevil exhibit an orderly pattern of feeding and oviposition activity on the leaders of open-growing white pine that can be readily followed throughout the season. On the other hand, in understory pine stands where weevil damage is negligible, it has been shown that there is no consistent pattern. Instead, the punctures may be distributed randomly over several years' growth of the main stem. Moreover, the amount of activity, as indicated by the number of punctures, is considerably reduced. These variations in the behaviour of adults in extreme habitats assume considerable importance when viewed with respect to survival of the population. In the exposed stand, they are associated with a survival ratio that permits population growth. In the shaded stand, however, they are associated with no survival. In both types of stand the insects are subject to a combination of microenvironmental and structural limitations that curtail their numbers. The exposed stands, however, are characterized by an abundance of leaders providing physical qualities within the preferred range of the insect, so that its behaviour and survival are regulated primarily by variations in the microenvironment of the habitat (Sullivan, 7). On the other hand, in shaded stands microenvironment and leader size combine to provide protection from weevil attack.

Whereas solar radiation exerts decided effects on the bark temperature of weevil habitats in open sites, the shading of understory pine leaders alters considerably the bark temperature and moisture relations of the habitat, because radiant heating by the sun is reduced in proportion to the amount of shade. The magnitude of these differences are such that they cannot be ignored as a major

factor regulating the amount of adult feeding and oviposition in shaded stands. In addition, in terms of the timing of these activities, it has been shown that they coincide with the period of canopy development, so that the magnitude of the differences in habitat microenvironment varies throughout the active period of the adults. Thus, quantitative studies aimed at forecasting differences in amount of these activities produce some interesting results. For example, during that part of the season coinciding with first oviposition and ambient weather conditions that permit a maximum amount of weevil activity, the magnitude of the differences in habitat microweather between the two sites accounts for reductions in feeding and oviposition in the shaded stand of about 30 and 40 per cent, respectively. These differences increase as the development of the overstory canopy reduces insolation, so that by the end of the season of adult activity, they stand at 45 and 80 per cent, respectively. The results indicate that the greater limitation is placed on oviposition activity and that the most critical period for infection of shaded stands, through oviposition, occurs just before the deciduous canopy begins to unfold. There are, however, two main reasons why a large amount of oviposition does not occur during this period. One is that only a small percentage of the population has reached the physiological state required for oviposition. By the time the majority of the population are capable of oviposition, the habitat microweather conditions serve to limit the amount of egg laying to about 45 per cent of that occurring in open sites during ideal weather conditions, and this is further reduced to 20 per cent by the end of the oviposition period. It is clear, however, that the microenvironment of the shaded habitats does not alone stop oviposition. The physical attributes of the shaded leaders are the second major factor limiting oviposition and larval survival, and hence contributing to the control of weevil populations in shaded stands. To expand this point, the variation in the oviposition pattern on exposed stems and on shaded stems is considered in terms of the ultimate success of the population.

On an exposed tree the insects reach the upper part of the leader through a positive response to temperature and light and a negative response to gravity (6). Subsequent activity includes feeding and oviposition that produces the characteristic frequency and distribution patterns indicated in Fig. 1A. These activities continue for about five weeks, with those eggs deposited at the upper part of the leader hatching first. Upon hatching, the young larvae, confined to a common feeding site, begin moving down the leader by feeding in a ring on the inner bark. External evidence of this is clearly indicated by a browning and drying out of the intact outer layer of bark. As a result of the method of adult attack, those larvae hatching later in the season are seldom hampered by a lack of food for their immediate requirements. Ultimate survival, however, depends on their obtaining and maintaining a position within the main feeding ring. When larvae are present in small numbers, or when individuals fail to contact the main feeding aggregate, they are pitch-drowned. Many larvae in overpopulated leaders die of starvation, but the success of the remainder is dependent upon a distribution of eggs that will lead to aggregations of larvae at a common feeding site (5).

On the other hand, in shaded habitats where the temperature and light differences between the upper and lower areas of the attacked portion of the main stem are very small, the adults reach the upper portion of the leader mainly through a response to gravity. This initial travel to the leader tip may be considered a basic characteristic of weevil behaviour, providing the insect with a starting point from which all subsequent movement associated with feeding and

oviposition behaviour takes place. The response is not, however, strong enough to hold them at this site if the physical characteristics of the leader are not suitable for oviposition and feeding. They respond to the unsatisfactory site by considerable movement up and down the main stem of the tree, so that feeding and oviposition punctures occur scattered over as many as five years' growth of the main stem. Following periods of inactivity, this behaviour pattern is repeated, i.e., repeated travel to and from the upper portion of the leader searching for a suitable site for feeding and oviposition. When this behaviour pattern is associated with the limitations placed on the amount of oviposition permitted by the habitat microenvironment, it is found that weevil females do not deposit a sufficient number of eggs in a localized area of the main stem to produce an aggregation of larvae, a characteristic essential to their survival.

It appears obvious that the physical characteristics of the leaders serve as a well defined indicator of susceptibility to weevil attack. Additional investigation is required, however, to determine why the insect selects particular leaders for oviposition. It is probable that the distribution of the eggs on the understory pine occurred because the bark of the leaders was not of sufficient thickness to permit a weevil female to make an oviposition outlet suitable for the deposition of an egg. This explanation does not, however, account for the limitations imposed by bark thickness of leaders greater than 11 mm. upper diameter, if, in fact, this is a true characteristic of weevil behaviour and not merely an artifact caused by the frequency of leaders in this size range. It is suggested that an investigation into the texture of bark of varying thickness might permit an appraisal of the quality of bark favourable to weevil attack.

Throughout this paper, the survival of *P. strobi* has been discussed in terms of its behaviour and activity in exposed and shaded stands of white pine. Although many of the observations were made in extreme habitats, in some requiring the use of introduced populations, it should be recognized that all weevils liberated into such areas react to the habitat conditions by leaving the stand before more than nominal damage has occurred. This occurs in stands with fully developed canopies of aspen when insolation at the level of the understory pine is reduced by 60 to 80 per cent during clear days. In other studies (Belyea and Sullivan, 1), the same relations existed when the canopy consisted of red oak. However, when insolation is reduced by only 25 to 50 per cent, as with a canopy of more widely spaced aspen, weevil damage is appreciable, but still only of the order of 10 per cent of that experienced by trees in the open. In these stands, leader vigour and microweather varied in relation to the amount of shade. Thus, the white pine trees, subjected to insolation more closely approaching fully exposed sites, provided leaders with physical characteristics more closely resembling those in heavily attacked stands. It is apparent, therefore, that in mixed stands, the amount of shade provided by the canopy determines the degree of protection afforded the understory pine. Although this will vary, depending on the species involved and site qualities, it should form a basis for future studies designed to examine means of managing white pine stands while maintaining weevil damage at a tolerable level.

**Summary**

The effect of weather and the physical attributes of white pine leaders on the behaviour and survival of the white pine weevil, *Pissodes strobi* Peck, in mixed stands was investigated near Chalk River, Ontario. Joint observations made in heavily weevilled open-growing stands, and shaded stands relatively free of weevil attack were designed to assess the relative importance of these factors in

limiting the successful invasion, by the weevil, of white pine stands growing as partially suppressed understory species.

In open-growing young stands of white pine, adults of the white pine weevil exhibit an orderly pattern of feeding and oviposition behaviour that is confined mainly to the previous year's growth of the main stem. The attack begins on the uppermost portion of the leader and progresses downwards throughout the season as the upper portions approach a puncture threshold. By the end of the season, roughly equal numbers of feeding and oviposition punctures are distributed evenly throughout much of the area of the leader that is attacked. In shaded stands, where damage is negligible, adults do not confine attack to the leader, but may feed and oviposit on as many as four- or five-years growth of the main stem. Equal numbers of feeding and oviposition punctures do not occur, nor is there any regularity to the distribution of the punctures on the main stem. Finally, the degree of attack is greatly reduced.

The shading of understory pine alters considerably the microenvironment of weevil habitats, since the radiant heating of the sun is reduced in proportion to the amount of shade. Since the season of oviposition and feeding coincides with the period of overstory canopy development, the magnitude of the differences in habitat microenvironments between exposed and shaded stands continually varies throughout the active period of the adults. In terms of bark temperature of oviposition sites, differences between exposed and shaded sites range from a minimum of about 3°C., at the time the shaded stems receive about 70 per cent of maximum insolation on clear days, to about 11°C., at the time the canopy is fully developed and the leaders receive only about 20 per cent of maximum insolation. The magnitude of the reductions in temperature and moisture relations of shaded habitats delimits the extent of such activities as feeding and, in particular, oviposition. In naturally occurring shaded stands where weevil damage is negligible, however, the microenvironment does not prohibit feeding or egg laying entirely.

Weevil adults also exhibit a preference for white pine leaders within a particular diameter range and bark within a certain thickness range: white pine stems having leaders devoid of these physical qualities are rejected. In shaded stands they provide an additional barrier to heavy weevilling.

The developmental success of *P. strobi* in exposed stands permits some population growth. In shaded stands, where weevil damage is negligible, second-generation adults are not provided, primarily because the females fail to deposit a sufficient number of eggs in a localized area of the main stem. Therefore, hatching larvae fail to aggregate at a common feeding site, a behavioral characteristic essential to survival: isolated individuals and small groups of larvae are generally pitch-drowned, because they are unable to make sufficient progress to stay ahead of the resin flow.

The results of this investigation indicate that the microenvironment and the physical attributes of the leaders in white pine stands determine the degree of protection from weevil attack. The relative importance of these factors varies in accordance with the level of exposure of the stands, hence the shade factor should be considered in studies designed to provide means of managing white pine stands to maintain *P. strobi* attack at a tolerable level.

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**References**

1. Belyea, R. M. and C. R. Sullivan. 1956. The white pine weevil: A review of current knowledge. *For. Chron.* 32: 58-67.
2. Graham, S. A. 1918. The white-pine weevil and its relation to second-growth white pine. *J. For.* 16: 192-202.
3. MacAloney, H. J. 1930. The white-pine weevil (*Pissodes strobi* Peck). Its biology and control. *N.Y. State Coll. For. Bull.* 3.
4. Peck, W. D. 1817. On the insects which destroy the young branches of the pear-tree, and the leading shoot of the weymouth-pine. *Mass. Agr. Jour.* 4: 205-211.
5. Sullivan, C. R. 1959. White pine weevil. *Canada Dept. Agr., For. Biol. Div. Bi-Mon. Prog. Rep.* 15 (2).
6. Sullivan, C. R. 1959. The effect of light and temperature on the behaviour of adults of the white pine weevil, *Pissodes strobi* Peck. *Can. Entomologist* 91: 213-232.
7. Sullivan, C. R. 1960. The effect of physical factors on the activity and development of adults and larvae of the white pine weevil, *Pissodes strobi* (Peck). *Can. Entomologist* 92: 732-745.
8. Taylor, R. L. 1929. The biology of the white pine weevil, *Pissodes strobi* (Peck), and a study of its insect parasites from an economic viewpoint. *Ent. Amer.* 9: 167-246.
9. Wellington, W. G. 1950. Effects of radiation on the temperatures of insectan habitats. *Sci. Agr.* 30: 209-234.
10. Wellington, W. G. 1957. The synoptic approach to studies of insects and climate. *Ann. Rev. Ent.* 2: 143-162.

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## A Simple and Inexpensive Apparatus for Photographing Events at Pre-set Intervals[1]

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During studies of the locomotory behaviour of blowfly adults, one of us (G.W.G.) developed a simple tilting-type actograph wherein an electrical circuit was opened or closed each time a fly moved from one end of a small cage to the other. Circuits from six such cages were connected to solenoid-activated pens on an event recorder so that movements in each cage were recorded as crosslines on the respective pen records. At peak activity, an individual fly may activate a pen up to 4,800 times during a 24-hour period. With six flies active at the same time, abstraction of a day's chart was a formidable and time consuming task. In analysing the data, activity counts over consecutive half-hour periods proved adequate, and some method was sought whereby half-hour activity records could be obtained. Six electrically operated counters were arranged so that they were activated by the closing of contacts attached to their corresponding pens. Thus, each time an actograph circuit was closed, a pen was activated producing a cross-line on the chart, and a count of fly activity was registered by a corresponding counter. To simplify the situation further, some method of automatically photographing the counter dials at half-hour intervals was required. The photographic apparatus subsequently developed proved to be simple, inexpensive, and reliable. Because it is adaptable for use in many situations requiring photographic records at pre-set intervals, details of its construction are reported herein.

[1]Contribution No. 734, Forest Entomology and Pathology Branch, Department of Forestry, Ottawa, Canada.

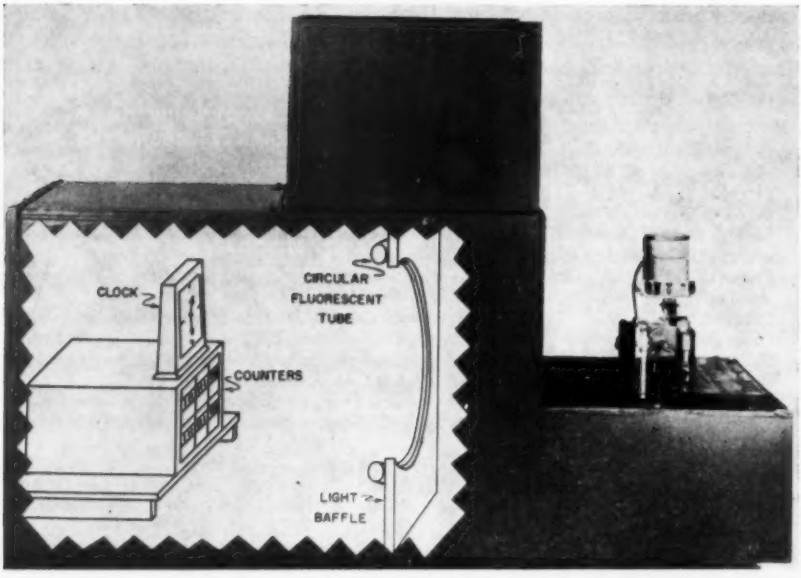


Fig. 1. Side view of the photographic apparatus with access door to the camera opened. The inset sketch shows the relative positions of the counters, time-check clock, and illuminating unit.

The case containing the counters and the apparatus designed to photograph them are shown in Fig. 1 with the access door to the camera shown in the "open" position. The case was constructed of half-inch plywood, with the outside dimensions measuring 13 by 15 by 36 inches. It rested on four suction cups that firmly gripped the supporting bench. As shown in the inset sketch in Fig. 1, the counters were mounted in a bank on a wooden shelf at the end of the case opposite the camera. A manually-wound alarm clock centred on the top of the counter bank provided a time check for each exposure. Access to the clock and counters was provided through a hinged lid in the top of the case and a removable panel forming the end of the case behind the counters. Illumination was provided by a 32W "Circline" fluorescent lamp mounted on a wooded baffle about nine inches from the face of the counters. The inside of the case on the counter side of the baffle was painted white to improve illumination, while on the samera side, it was painted flat black to minimize reflection. The position of the lamp and the baffle along the length of the case was dependent upon the acceptance angle of the camera lens and the size of the area to be photographed. The unit comprising the camera, film drive motor, and solenoids for cocking and releasing the shutter was mounted in the end of the case opposite the counters.

The camera was a 35 mm. Kodak "Retinette", masked to take half-frame exposures on a standard 36-exposure roll of Kodak Plus-X film. The exposure-counting component of the camera was altered to allow continuous winding as well as shutter release at any desired interval. A small, synchronous motor, with a shaft speed of 1 r.p.h., was mounted directly above the film-drive spindle, and connected to it through a prong and socket linkage (Fig. 2). Revolving at 1 r.p.h., this motor wound the film through the camera so slowly that exposures taken at 1/50 sec. with an f-8 aperture setting were clear and sharp. At this

Fig. 2. Frontal view of the camera, film-drive motor, and shutter-cocking and -release solenoids of the photographic apparatus.

film-drive speed, a 36-exposure cassette contained enough film for 26 hours of continuous operation. The film-drive motor was lifted vertically and freed from its linkage with the film-drive spindle on the camera during film changes, the whole operation requiring less than two minutes. No records were lost during this period because the film was changed between exposures and the counters continued to operate during film changes. A 110V solenoid, of the type used to control the water pumps in automatic washing machines, was used to cock the shutter. As shown in Fig. 2, this solenoid was mounted at an angle below the camera platform with the plunger connected to the cocking lever on the camera by means of a light, flexible chain. A coil spring attached to the chain protected the cocking mechanism from undue pressure, and obviated the necessity of critically adjusting the position of the solenoid to provide a consistent cocking-force. The shutter-release lever on the camera was connected directly to the plunger of a smaller solenoid operating on 14V DC.

Two mercury switches, mounted so that they could be tipped easily to close the circuits, activated the shutter- and cocking-solenoids (Fig. 3). A brass bushing attached to the shaft of a small, synchronous motor supported two pairs of arms of different lengths, set at 90° to each other and projecting over the switches. The motor turned this assembly at 1 r.p.h., and adjustable rods at right-angles to the arms were set to tip each of the switches at half-hour intervals with a lag of approximately 15 minutes between the operation of each switch. By critically adjusting the length of these rods, the switches could be set to close the circuits within ± ¼ min. of the 30-minute cycle of operation. At the beginning of an

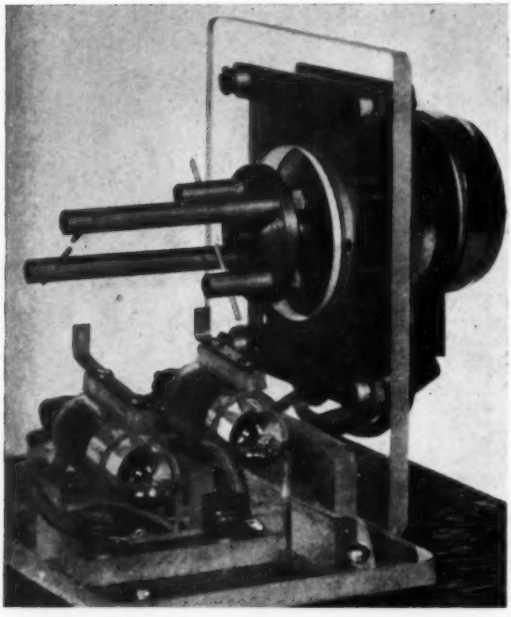

Fig. 3. Timing switches, and timing-switch motor used to control the operation of the shutter-cocking and -release solenoids in the photographic apparatus.

experiment the shutter-release switch was set to operate on the hour and on the half-hour. Thus, in one revolution of the timing-switch motor, the shutter would be released at, for example, 1300 hr., the camera cocked at 1315 hr., the shutter released at 1330 hr., and the camera cocked again at 1345 hr.

A sample of the film record is shown in Fig. 4. For abstracting, it was necessary only to read the numbers from the counter photographs using a small magnifier with the film set on a white background or over a light table. By subtraction, the activity occurring during consecutive half-hour periods was obtained for each of the actograph channels. Using this method, data for a 24-hour period, which took from 10 to 12 hours to abstract by counting the pulses on the event recorder chart, could be abstracted in from two to three hours. The

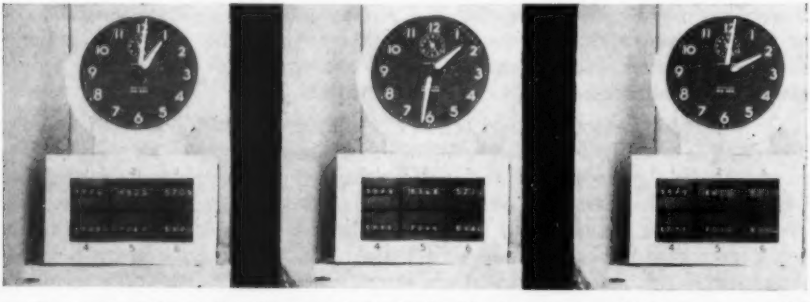

Fig. 4. Samples of the film record obtained with the photographic apparatus at 1300, 1330, and 1400 hr. during an experiment.

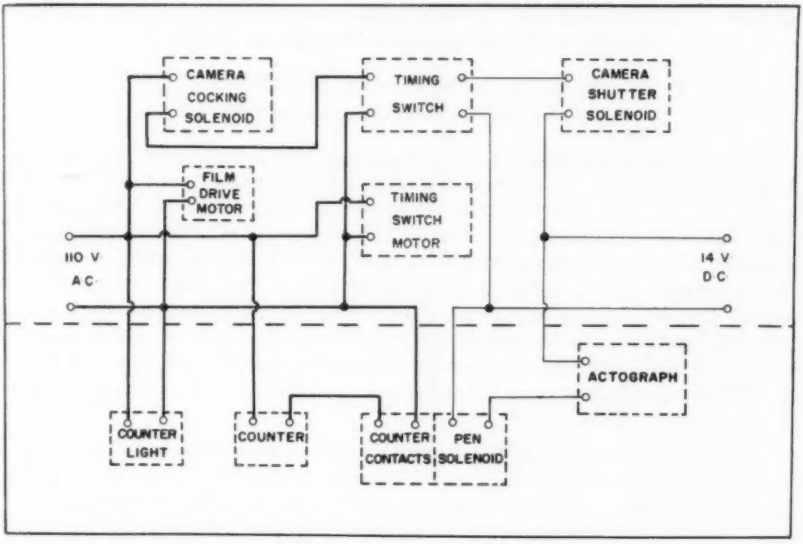


Fig. 5. Schematic wiring diagram of the activity recording apparatus.

time saved more than justified the relatively small expense of the apparatus. In addition, no sensitivity was lost, since more detailed abstractions of points of particular interest could be obtained from the event recorder charts.

A schematic wiring diagram of this apparatus is shown in Fig. 5. A broken line through the lower third of the figure separates the components used in recording blowfly activity from the actual photographing mechanism. Removal of these components leaves the circuit of the photographing mechanism intact and operable.

Although designed for a specific job, the photographing mechanism is easily adaptable to a number of different roles. Its use in simplified time-lapse photography, where a moving picture record is not required, is obvious. Necessary changes in the speed of the film-drive motor and the timing mechanism for the operation of the shutter-cocking and -release solenoids are easily made. The apparatus is especially suited to the photographing of insects in a choice-chamber at pre-set intervals, or in studies of the group behaviour of insects exhibiting diurnal rhythms in activity. With minor modifications, it could be set up to record cloud cover at hourly or half-hourly intervals. Over a 3-month period of continuous operation, the apparatus has functioned flawlessly, the only maintenance required being daily film changes and winding of the time-check clock.

The main components of the photographic unit are: 1, Camera—most cheap 35 mm. cameras could be adapted for use in this apparatus; 2, Synchronous motors—Hurst RSM reversible motor, 1 r.p.h., Hurst Manufacturing Corp., Princeton, Indiana; 3, Timing switches—Honeywell, AS454A18, at most electrical stores; 4, Shutter-cocking solenoid—Bendix water pump solenoid with return arm, spring, and pivot pin, at most appliance repair shops. The shutter-release solenoid was made in the laboratory. The remainder of the materials are usually in stock in most laboratories. The overall cost of parts for the apparatus should not exceed eighty-five dollars.

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# Factors Influencing the Distribution of Overwintering Ambrosia Beetles, *Trypodendron lineatum* (Oliv.)[1]

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Previous work by Kinghorn and Chapman (1959) has shown that in coastal British Columbia, the ambrosia beetle *Trypodendron lineatum* hibernates in the forest litter or duff at various distances within forest edges in the vicinity of brood logs. It was pointed out that further study was required to determine the characteristics of the optimum hibernation sites. It was mentioned that stand density, shade, aspect, slope, and the nature of the duff might be factors controlling the selection of the place of hibernation. The base of trees and the relatively deeper duff, characteristic of this situation, was reported to be the location of the larger populations of hibernating beetles although the level of population was found to vary greatly both from tree to tree and in depth within different forest edges.

The present study describes several aspects of hibernation. The movement of the beetles from brood-logs to hibernation within the edge of an adjacent forest was studied. The nature of the hibernation sites, in the duff and in the bark of trees, was investigated to determine whether the depth of the duff or the thickness and roughness of the tree bark were factors influencing the number of beetles which select these sites. Habitats within the forest at the base of trees, between trees, under salal (*Gaultheria shallon* Pursh.), and in open areas were studied to measure their relationship to hibernation of *Trypodendron*. In habitats having similar characteristics, large variations in the number of beetles were found both at different distances from the forest edge and at different parts of the forest at the same distance from the edge of the stand. These variations in number of beetles were studied in relation to the amount of shelter and incident light penetrating to the ground through the forest canopy.

The forest stand in which these studies were carried out was mature and had marked variation in the density of the main crown canopy. It consisted predominantly of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) with a few western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.), western red cedar (*Thuja plicata* Don) and western white pine (*Pinus monticola* Dougl.). Small patches of second growth hemlock and cedar provided a dense canopy contrasting with the lighter shade beneath the large, high crowns of the clear-boled mature trees. Low shade occurred under scattered small trees growing as understory below the main canopy. The stand was about 1,300 feet long and 300 feet wide, bounded by an open roadway on one side and cleared areas on the other three sides (Figure 1).

## Methods

The investigation was begun in August, 1959, at the Northwest Bay logging division of MacMillan, Bloedel and Powell River Company Limited near Parksville, British Columbia. Two 20-acre blocks of timber had been felled in December and January of the previous winter. The logs were left on the ground for *Trypodendron* studies until November. By this time the broods resulting from the spring beetle attacks had left the logs to hibernate.

The data on the distribution of hibernating beetles were obtained by collecting one-square-foot (12 by 12 inch) samples from the duff and from the bark at

[1]Contribution No. 729, Forest Biology Division, Department of Forestry, Ottawa, Canada.

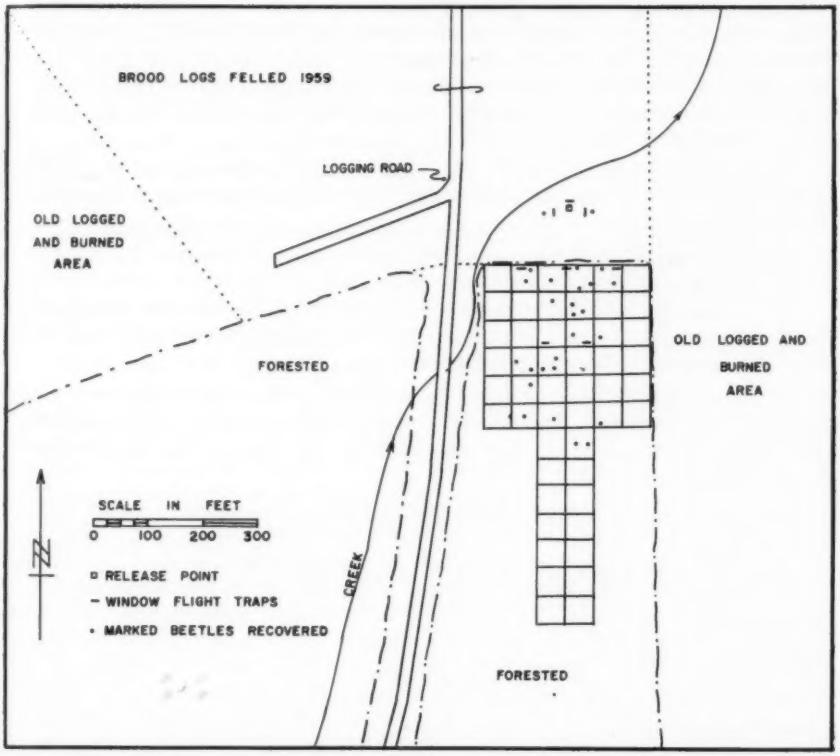


Fig. 1. Sampling area at Northwest Bay showing the point of releasing marked beetles, location of marked beetles recovered in hibernation, the position of window flight traps and the forested area adjacent to the brood logs.

the base of trees. The samples taken from the ground contained all material, including moss, down to the compacted organic or mineral layers. The samples from the trees contained all bark to the base of the deepest fissures, leaving a smooth surface in which no hibernating beetles would be missed. A few bark samples were taken at various heights above the ground by felling or climbing the tree. Samples were stored at outdoor temperatures in plastic bags for one to two weeks until beetles could be recovered at the field laboratory. No mortality due to storage was apparent.

Beetles were recovered by the heated pan method described earlier (Hadorn, 1933, and Kinghorn and Chapman, 1959). The time required for recovery from samples was much reduced by first removing fine and coarse material with the aid of a three-screen mechanical vibrator. After five minutes sifting, the duff containing beetles was less than half the original volume. Prior to sifting, the volume of duff and moss in each sample was measured in cubic inches. The samples of bark were treated in a similar manner except that the bark was first broken into small pieces. Beetles killed when the bark was broken could not be recovered by the heated pan method. Upon immersion of the sifted bark in a mixture of oil and water, damaged beetles floated at the interface of the two liquids where they could be counted.

Fifty intensively sampled plots, 50 feet by 50 feet, were marked out in the timber adjacent to the cleared area containing logs infested by *Trypodendron*. Thirty-six of the plots were placed contiguously in an area 300 feet by 300 feet. The other fourteen plots adjoined the centre portion of the first block so as to extend the area sampled to 650 feet from the forest edge which was the nearest source of emerging beetles (Figure 1).

Every sample was identified by its location and by the type of forest floor habitat from which it was gathered. The following habitats were distinguished:

1. Adjoining base of trees on south side (away from clearing).
2. Adjoining base of trees on north side (toward clearing).
3. Under salal more than five feet from a tree.
3. On bare ground with only moss cover and more than five feet from a tree.
5. Under various types of cover such as windfall, logs, and small trees with a diameter of less than six inches.

A further classification of the samples taken at the base of trees was made by noting whether they were sheltered above from branches within ten feet. The samples from the bark were identified by tree species, the height above ground, and the location.

The variations in density of the crown canopy and other forms of shelter were indicated by the amount of incident light reaching the ground. The light was recorded with a photometer capable of recording light intensity from one to 500 foot-candles. Light was measured along lines at 25-foot intervals in the area of intensive sampling. From the grid of 144 light measurements, zones of equal light intensity were sketched on a map showing the positions of the larger trees and the samples. These light measurements were taken at a height of six feet above ground. In addition, light was measured at ground-level over samples taken on opposite sides of 87 trees; in each case the light was also recorded at ground level three feet from the tree trunks. The light readings used for comparison of relative magnitude were taken as quickly as possible under uniform cloud conditions to reduce error due to changes in light not caused by differences in forest cover.

Movement of beetles from the brood logs into the forest edge was indicated by the use of flight traps, emergence traps, and by releasing marked beetles. The flight traps were of the window type described by Chapman and Kinghorn (1955, 1958). These were mounted about five feet above ground along the edge of the forest, 150 feet within the forest, and on three sides of the position from which marked beetles were released (Figure 1). The emergence traps consisted of aluminum rings about 1.5 inches in diameter and one inch deep. These were fastened on logs over the beetle holes and covered with cloth secured by an elastic band. Emerging beetles were retained in the traps as they left their brood galleries.

More than 30,000 beetles, collected as they emerged from heavily infested wood, were marked with fluorescent paint. A spot of fast-drying paint was placed either on the beetle's pronotum or on one elytron. All were released from one point in the cleared area about 100 feet from the edge of the forest to be intensively sampled later. As the beetles were released, it was observed that some were in a weak condition and markings on others had vanished. While it is impossible to know the total loss through these causes, it is estimated that less than one-half of the beetles left the release point bearing effective markings.

## Results

*Movement of Beetles into Hibernation*

The beetles began to leave the brood logs in small numbers and fly into the forest edge during the second week of July. Records of the number of beetles leaving and the number being taken in the flight traps at the forest edge indicated that considerable movement occurred until September 15. A few beetles continued to leave the brood logs after September 15 and enter the forest as late as October 21, but these constituted only seven per cent of the population trapped.

The first duff samples were taken on August 25. Nearly 500 samples collected before September 15 did not represent the full hibernating population as determined by comparison with paired samples taken in October and November. All samples collected after September 15 were considered to adequately represent the whole hibernating population.

The marked beetles, when released on a log about 100 feet from the forest were observed to fly upward to about 50 feet before moving very far in any lateral direction. Many of these beetles were then seen to turn south toward the forest although they could not be observed for a distance of more than about 100 feet. There is some evidence from these observations that a number of the beetles enter the edge of the forest flying just below the tree crowns. Those beetles caught in the flight traps at the forest edge were, however, flying at about five feet from the ground.

Eight marked beetles were recovered in the flight traps, five at the forest edge and three in two traps placed on either side of the release point. None were recovered from the trap on the side of the release point away from the forest. From the duff samples collected in the forest, 23 marked beetles were recovered at distances of from 100 to 450 feet from the release position. All but one of these were found within a strip 200 feet wide centred on the most direct line from the release point into the forest. Some of the marked beetles did not move from the release point because samples containing 50 or more marked beetles were found in duff beneath the log where they were liberated. Under other logs from which large broods of beetles had emerged in the same area, the samples averaged only two beetles. The distribution of the recovered marked beetles indicated that their dispersal was centred around the most direct line into the forest and they were generally found among the larger concentrations of the sampled population in this area.

Three other forest edges at distances of about one quarter of a mile from the brood logs were sampled; an average of less than one beetle per sample was found in 33 samples taken at the base of trees. One hundred and ninety similar samples collected in the forest adjacent to the brood logs, contained a mean of 27 beetles. Most of the beetles apparently hibernated within the edge of the forest nearest to the brood logs although dispersal to a distance could not be adequately measured.

*The Hibernating Sites*

Prior to this study it was thought that this insect hibernated only in the ground, but it was soon discovered that large numbers of beetles were hibernating in the bark of standing trees. A few details of this phenomenon have previously been noted by Kinghorn and Dyer (1960). The relationship of the number of beetles hibernating in the bark at the base of trees to the number hibernating in the duff at the base of the same trees is illustrated in Figure 2. Slightly more than half as many beetles may be expected to hibernate in the basal square foot

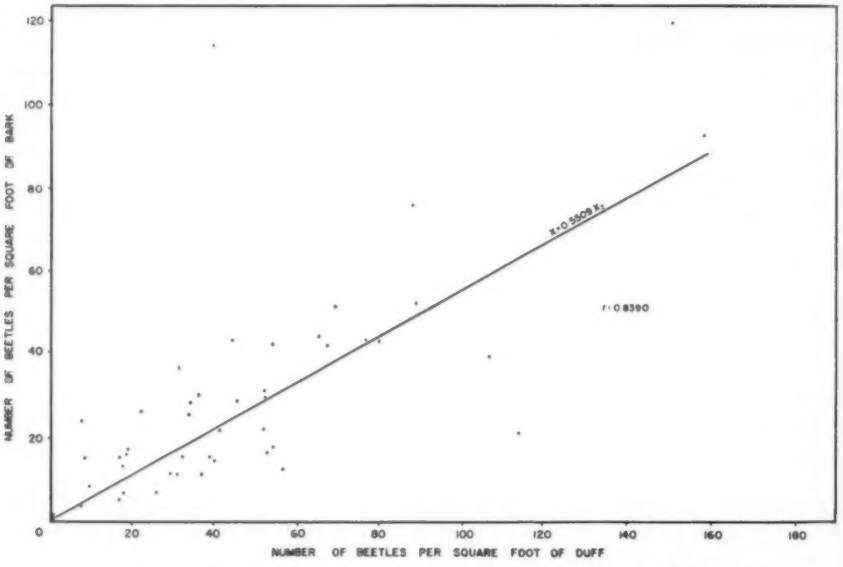


Fig. 2. The relationship between the number of hibernating *Trypodendron* in the square foot of duff at the tree base and in the contiguous bark on the base of the tree.

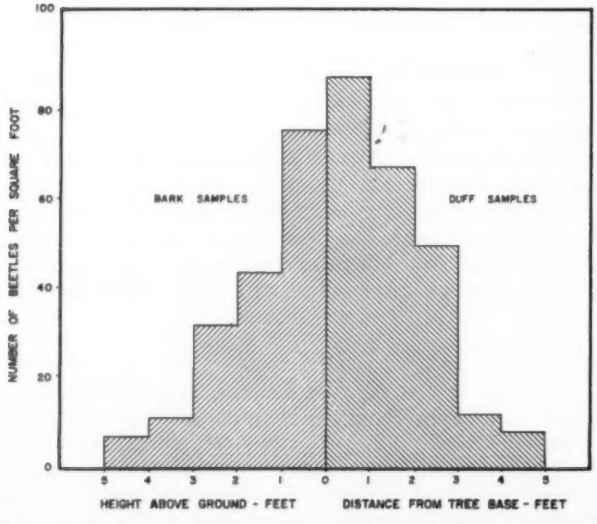


Fig. 3. The distribution of hibernating *Trypodendron* in the bark and in the duff at the base of a tree.

TABLE I
Bark samples and contiguous duff samples from the base of trees with thin and thick bark

| Tree species | Type of bark | Number of samples | Mean number of beetles per square foot of duff | Mean number of beetles per square foot of bark | Per cent beetles in bark to beetles in duff |
|---|---|---|---|---|---|
| Western hemlock | thin | 12 | 59.7 | 35.5 | 59.5 |
| Douglas fir | very thick | 27 | 43.6 | 25.3 | 58.0 |
| Western white pine | thin | 4 | 34.2 | 16.2 | 47.4 |
| Western red cedar | very thin | 1 | 45.0 | 28.0 | 62.2 |

of bark as hibernate in the adjoining square foot of duff. The distribution of beetles from the base of an individual tree is illustrated in Figure 3. In this particular case the number of beetles hibernating in the bark more nearly equalled the number in the duff, but the typical reduction in density away from the tree base is evident. Relatively few beetles hibernate in the duff more than four feet from a tree base except when other types of low shelter and shade occur. On one tree a beetle was found hibernating in the bark at a height of fifty feet although most of the population occurred at less than five feet from the ground.

The beetles had frequently bored into the bark, particularly of the thinner barked trees, although none had reached the cambium. In some cases several beetles had hibernated in one enlarged niche, having entered through the same hole. The nature of the bark of different tree species did not in itself seem to govern the relative number of hibernating beetles. The mean number of beetles found in the duff at the bases was compared with the mean number found in the adjacent bark of trees with various bark types (Table I). The very thin, smooth bark of cedar and the relatively thin bark of hemlock contained about 60 per cent as many beetles as did the adjacent sample of duff. Approximately the same percentage of hibernating beetles was found in the bark of Douglas fir although the bark on these mature trees was extremely thick, and deeply fissured. In other words, for every 10 beetles found in the duff sample six were found in the adjacent bark regardless of the bark type or tree species.

The volume of duff in each sample was measured to obtain information on its depth as it might be related to the number of hibernating beetles. Seventy-six samples taken in similar habitats at the base of trees were divided into three classes of beetle numbers (Table II). The average volume of duff and moss was

TABLE II
The depth of duff based on the volume per square foot sample and the number of *Trypodendron* per square foot hibernating at the base of trees

| Number of beetles | Number of samples | Mean volume in cubic inches | | | Mean depth in inches |
|---|---|---|---|---|---|
| | | Duff | Moss | Total | |
| 0 - 19 | 24 | 273 | 34 | 307 | 2.13 |
| 20 - 39 | 26 | 277 | 25 | 302 | 2.10 |
| 40 - 159 | 26 | 263 | 39 | 302 | 2.10 |

almost constant for each size of beetle population (coeff. of variation 23-29 per cent). The mean volume of duff without moss was actually least in samples containing the largest number of beetles. The depth of the duff did not appear to affect the number of beetles which hibernated in it under the conditions of moisture, shade, and aspect prevailing in this particular forest.

Fifty-one selected samples taken at the bases of trees in the autumn of 1959 contained a total of 1,577 beetles. Samples were collected adjacent to these on June 29, 1960, to determine whether any beetles remained in hibernation after normal spring flight had apparently taken place. Four living beetles and 11 cadavers were found, representing 0.25 and 0.7 per cent, respectively, of the original hibernating population in the adjacent samples. Although no search was made for fragments of dead beetles, winter mortality was apparently very low and the number of living beetles remaining in hibernation at the end of June was insignificant. Furthermore the remaining living beetles might have left the duff later in the summer or have subsequently died. Therefore the probability of *Trypodendron* remaining in hibernation for more than one season seems remote under the conditions studied.

*The Influence of Habitats*

Five different habitats in the forest were distinguished by their physical characteristics. The number of samples taken after September 15 and the mean number of beetles per sample for each of these habitats throughout an area 300 feet in depth from the forest edge are listed in Table III. At the five per cent level, significantly more beetles were at the base of trees on the south side away from the forest edge than either at the usually more exposed north side or beneath the shelter of windfalls, logs or small trees. Very few beetles were found beneath salal or in open moss-covered areas; the mean number of beetles in these habitats was significantly less than the number at either side of the tree base, or under windfalls, logs and small trees. The difference between the mean numbers found under salal and in open moss-covered ground was not significant at the five per cent level.

*The Influence of Incident Light*

In Table IV the mean number of beetles is listed for all samples taken at the base of trees on the side away from the edge of the forest, throughout an area 300 feet in width and 250 feet in depth from the forest edge. The samples which had shelter from low branches contained significantly greater numbers of beetles at the one per cent level than did those without such shelter. Of the samples which had shelter from low branches, those from zones of lower incident light contained significantly greater numbers of beetles at the one per cent level than those from zones of higher incident light. Of the samples without shelter from low branches, those from the zones of lower light averaged more beetles than samples from the higher light zones, but the difference was not significant at the five per cent level.

The number of beetles which hibernated at the base of trees was greater than the number in the adjacent sample one foot away from the tree base (Figure 4). Measurements of incident light at the base and at three feet from the base of 87 trees showed that in 84 cases the light was lower at the tree base. Light measurements in the four cardinal directions around six trees indicate a reduction in light intensity toward the tree base from a distance of five feet (Figure 5). This gradient from higher to lower light toward the base of the tree coincides with the change from smaller to larger populations of hibernating beetles (Figure 3).

TABLE III
Mean number of *Trypodendron* per square foot found in five different forest habitats within the forest

| Habitat | Number of samples | Number of beetles |
|---|---|---|
| Base of trees away from the forest edge | 227 | 24.9 |
| Base of trees toward the forest edge | 37 | 16.0 |
| Under windfelled trees and small trees | 72 | 17.0 |
| Under salal cover | 40 | 3.6 |
| Open ground with moss cover | 40 | 1.9 |

As stated before, the average number of beetles which hibernated on the south sides of trees away from the forest edge was significantly greater than the number at the north sides. Also the side of the tree away from the forest edge was usually darker than the side toward the clearing. To clarify this point 87 paired samples were taken at the opposite sides of each tree. In 26 cases the north side of the tree toward the forest edge was actually the darker of the two and yielded a significantly larger number of beetles. Therefore, it was not surprising to find that the correlation coefficient between paired samples was higher (0.650) when the pairs were grouped by relative light intensity than when grouped by relative orientation to the forest edge (0.467).

In this particular situation the higher light intensity emanating from the clearing was offset by its northerly position relative to the sheltering forest; sunlight from the south tended to equalize the light intensity on both sides of the trees. In a situation where the brood logs were in a clearing to the south of a forest, one would expect the sides of trees away from the margin to be more consistently darker (and hence would harbour more hibernating beetles) than the sides facing the clearing.

A further relationship between light and the number of beetles in hibernation is illustrated in Figure 6. The paired samples from opposite sides of the tree base were divided into two nearly equal groups comprising those with large differences of light and those with small light differences between the opposite sides of the tree. The larger differences in the number of beetles occurred where there were large differences of light, and the smaller differences in numbers of beetles were found where there were small light differences. The correlation coefficient was also higher between samples with the larger light differences.

*Distance from the Forest Edge and Light Zones*

Large variations have been noted in the number of beetles hibernating in similar habitats at various distances within the forest edge. It has been found

TABLE IV
The effect of close shelter and incident light on the density of hibernating *Trypodendron* in the duff at the base of trees

| | Close shelter | | No close shelter | |
|---|---|---|---|---|
| | Low light zone | High light zone | Low light zone | High light zone |
| Number of samples | 45 | 41 | 47 | 57 |
| Mean number of beetles per square foot | 44.5 | 29.7 | 21.4 | 15.9 |

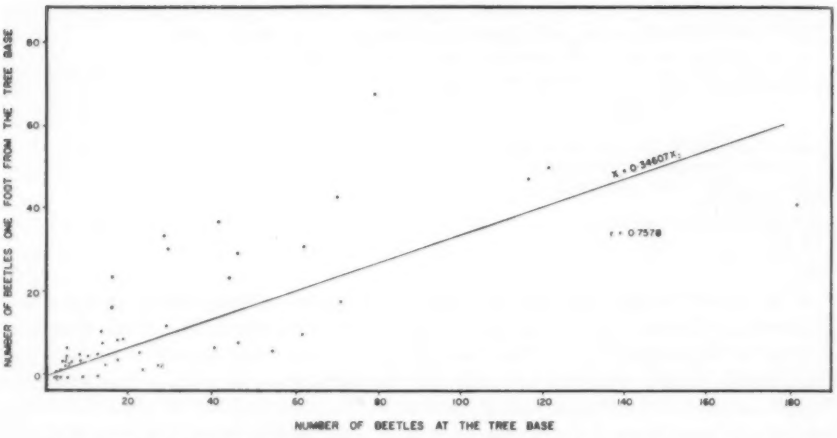


Fig. 4. The relationship between the number of *Trypodendron* per square foot of duff at the base of the tree and the number one foot away from the tree base.

that the largest number of beetles may occur at distances of 50 to more than 250 feet in different transects within the same forest and in different forest stands. Within some forest edges there may be two or more distinct areas of relatively high population at different depths into the stand.

Light intensities were measured at 25-foot intervals from the forest edge on four transects crossing the mid-points of the four centremost lines of plots. Average numbers of beetles at the base of trees in each plot and the corresponding light measurements were plotted against the distance from the common forest

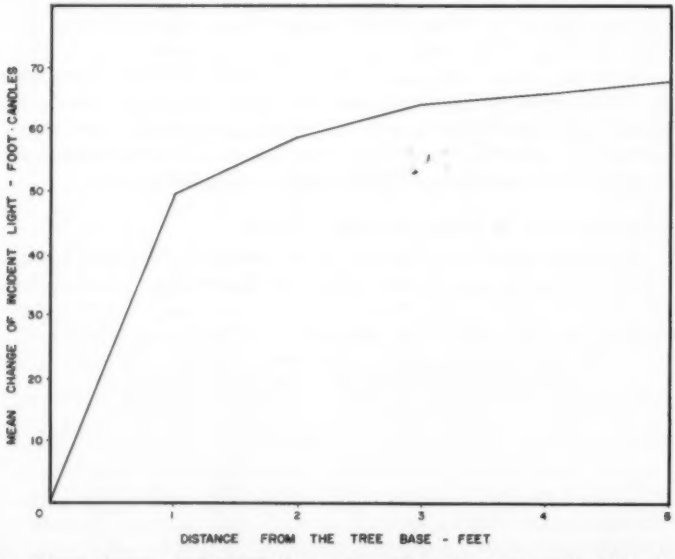


Fig. 5. Mean changes in incident light measured in the four cardinal directions from the bases of six mature Douglas fir trees at Northwest Bay.

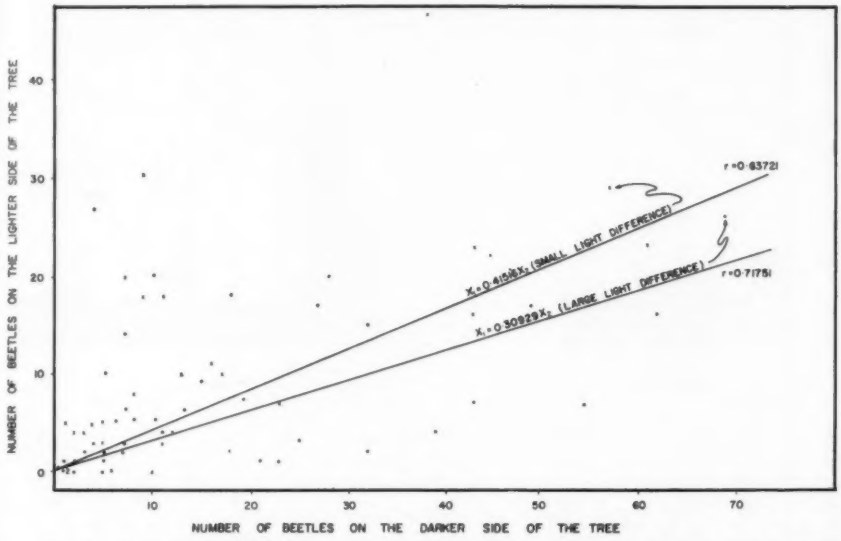


Fig. 6. Two relationships between the number of *Trypodendron* in paired duff samples taken at the opposite sides of the bases of trees where the light difference between sample pairs is large and where it is small.

edge (Figure 7). There were great variations in the light intensity on each of the transects at identical distances from the edge of the stand. On each transect the number of beetles was relatively high in a zone where the beetles, as they flew into the forest, would have encountered the first sharp reduction in light. Others obviously continued to fly through the first zone of relative darkness, and through an opening in the stand that was relatively bright, but finally settled in the next zone characterized by relative darkness. The data for Transect 4, Figure 7, best illustrate this secondary zone of high population as it relates to relative light intensity.

In the Nanaimo River drainage two different forest stands were sampled for hibernating beetles at 50-foot intervals on transects 100 feet wide extending from the edge of the forest into the stand. Incident light measurements were taken at 25-foot intervals along the centre line of each transect. The mean number of beetles per square foot of duff at the base of trees was plotted along with the light measurements (Figure 8). The optimum hibernation occurred at approximately 125 feet from the forest edge in one stand and at about 200 feet from the edge in the other. A gradient from high to low light occurred from the forest edge to a depth of 150 feet in the first stand and a more slowly changing gradient was found to 250 feet from the edge in the second. In both stands the largest number of beetles hibernated at the position where the light first dropped to its lowest point.

## Discussion

*Trypodendron* spends nearly two-thirds of its annual life cycle in hibernation and therefore a thorough understanding of this phase is of considerable importance. The rather long period from the middle of July until October, during which individuals of the population flew from the brood logs to hiber-

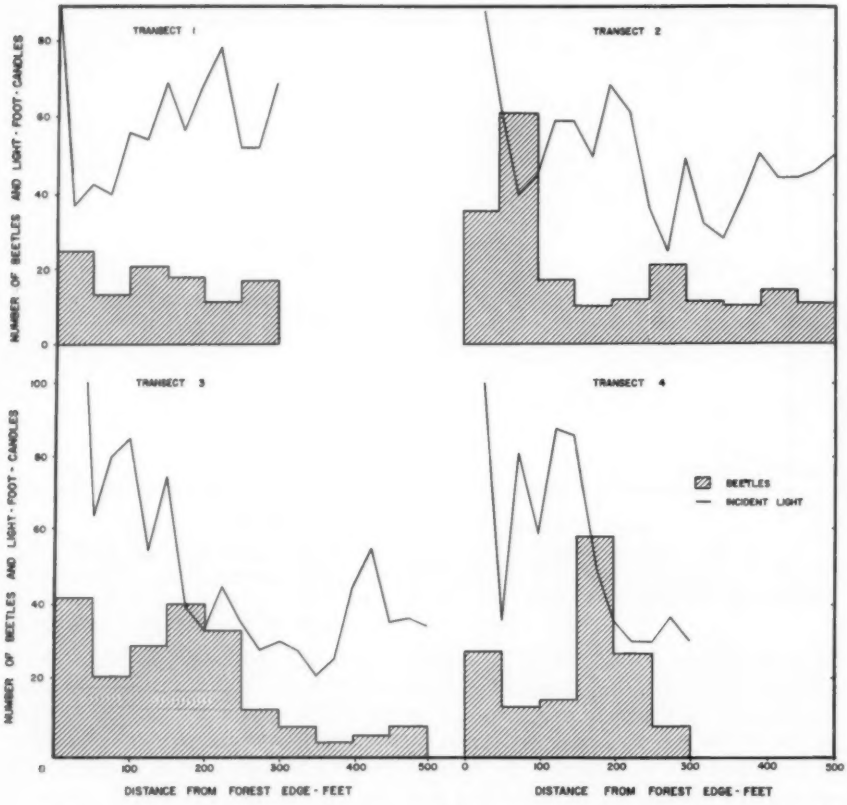


Fig. 7. Numbers of hibernating *Trypodendron* in relation to changes in incident light intensity and distance from the forest edge. Northwest Bay.

nation, was probably due to the various dates of the spring gallery establishment and the differences in rate of development of broods in various types of log material under different conditions of exposure and aspect. The flight to hibernation does not, under most field conditions, expose the beetles to prolonged hazard from predation, exhaustion, or adverse weather because the distance is usually short and the flight apparently direct to the nearest standing forest. Forest edges are usually close to the felled areas of the previous autumn in most logging situations in coastal British Columbia.

The hibernation sites in the forest duff and in the bark on the base of trees were quite variable in their physical nature. The beetles were found hibernating in both the hard thin bark on the base of some species of trees and in the adjacent deep, soft duff. Apparently the medium in which they choose to hibernate may vary greatly as long as it provides cover and darkness after entry. In the cases of hibernation in thin bark, the beetles could not find sufficient cover in the bark crevices and actually had to bore niches into the inner bark for hibernation. Although the hibernation sites where most beetles have been found offer a good deal of protection from climatic extremes, it would appear that the thin bark of

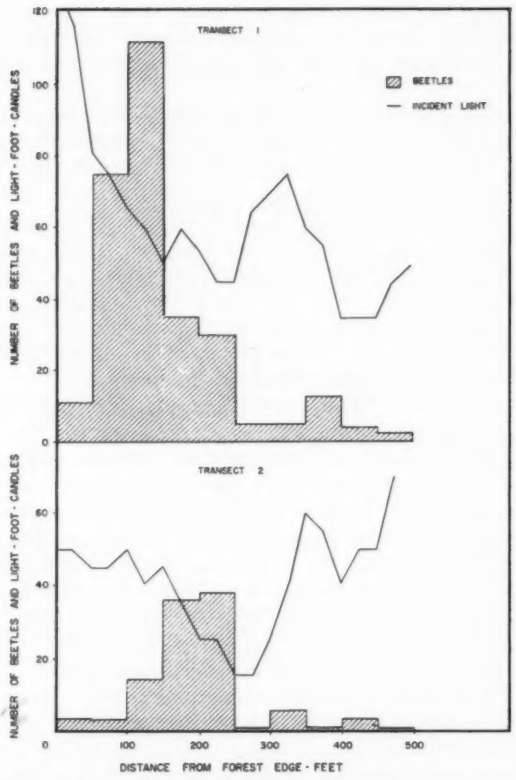


Fig. 8. Numbers of hibernating *Trypodendron* in relation to changes in incident light intensity and distance from the forest edge. Nanaimo River.

some trees affords much less protection than thick bark or deep duff. The habit of seeking zones of relative darkness, however, ensures that the largest part of the population hibernates under the most dense part of the forest cover.

Few beetles hibernated under salal cover. Although this habitat is very dark, the light immediately above and around it may be quite intense. It does not present a gradation from higher to lower light as is the case of a standing tree, but forms an abrupt change only near ground level. Dense salal characteristically occurs in the better lighted parts of the forest and therefore would seldom be present in the lowest light zones. Salal growing at the base of a tree does, however, increase the shade and, as Chapman (1960) shows, may influence the distribution of beetles around a single tree.

The different zones of incident light intensity are formed by the different densities of the crown canopy at all levels. This pattern of light characteristically changes from high light intensity at the forest edge to lower intensity within the stand, but this change may be rapid or gradual and also may reverse itself in a stand with large crown openings. The pattern of light apparently affects the beetle's selection of its hibernation habitat as it flies into the forest. A zone of low light which occurs close to the forest edge influences a larger number of hibernating beetles than does a second zone of equal darkness farther in the stand.

A forest which does not have a zone of low light near the edge has maximum density of hibernating beetles at a greater distance into the stand. Similarly, the darkest habitats within the low light zones contain the largest number of beetles.

This phenomenon seems to explain the maximum concentration of hibernating *Trypodendron* found by Hadorn (1933) at less than fifty feet from the edge of a young, dense forest. In such a forest it is likely that the intensity of incident light dropped rapidly within the first fifty feet to its lowest point, and if the stand was uniformly stocked, the amount of light would remain low farther from the edge. In the tall, mature, somewhat open stands investigated in this study the light from the forest edge penetrated much farther into the stand except where a denser understory of young trees occurred. The maximum numbers of hibernating beetles were found at more than two hundred feet from the edge of one mature forest where the intensity of incident light was not rapidly lowered by a continuous, dense crown canopy.

Investigations of the distribution of hibernating cotton boll weevil (Fye *et al.*, 1959) show that there is evidence that when these weevils fly into the woods from a cotton field to hibernate, they reach the ground on the far side of an intercepting tree or bush and apparently remain there. It was also found that where trees or bushes on the sampled swath were fewest, the weevils were found hibernating in peak populations almost 100 feet deeper into the woods than on other swaths. This is remarkably similar to some aspects of *Trypodendron* behaviour because the parts of the forest with the fewest trees and the highest light intensity had the peak populations hibernating farthest from the forest edge. *Trypodendron* also is found in the largest numbers behind trees on the side away from the forest edge when this side has the least light.

Although *Trypodendron* is apparently dominantly photo-positive when emerging from its brood gallery, it seems to lose this dominance during flight when seeking hibernation (Graham 1959). The action of the beetles in flight as they enter the forest has not been studied adequately yet, but from the distribution of hibernating beetles it seems probable that they follow gradients of lessening light while flying down toward the ground where they hibernate in the darkest habitat at, or near ground level. Where changes of gradient to increasing light are encountered it appears that they continue to fly deeper into the stand until the next zone of lower light occurs. This suggestion is based on the observation that beetles fly into the edge of the forest at heights from five feet up to about the base of the tree crowns and are found in large concentrations in hibernation near the end of each zone of low light, with the largest numbers in the nearest zone to the forest edge and in the darkest habitats.

## Summary

Most *Trypodendron*, upon emerging from the brood logs during July, August, and September, fly directly to the nearest standing forest to hibernate. Although the data from flight traps indicate that beetles were entering the forest before July 16, they continued to fly to hibernation in large numbers until September 15 and a few hibernated as late as October 21 in the area studied.

The nature of the duff and bark in which these beetles hibernate does not seem to be a factor in determining relative population density. Large populations were found in deep, as well as in relatively shallow duff. Both thick, heavily-fissured bark, and thin, smooth bark harboured large numbers of beetles.

The density of the forest canopy and the added shelter of the various habitats within the stand, control the relative amount of light reaching the forest floor.

Although these physical characteristics of the forest are correlated with the concentration of the hibernating beetle population, the corresponding light changes can be measured more accurately and are more closely related to the differences in population density than characteristics of the forest. The optimum hibernating sites are at positions of lowest incident light near the end of each gradient from the higher light at the open forest edge to the lower light within the stand.

**Acknowledgments**

We wish to thank Messrs. M. Jackson and G. Richardson for their assistance in carrying out this study. Thanks are also extended to Mr. R. R. Lejeune and Dr. J. A. Chapman, Forest Biology Laboratory, Victoria, for their constructive criticism of the manuscript.

**References**

Chapman, J. A. 1960. The distribution of overwintering *Trypodendron* (Coleoptera, Scolytidae) around a single tree in relation to forest litter variability. *Proc. Ent. Soc.* of *B. C.* 57: 3-6.

Chapman, J. A. and E. D. A. Dyer. 1960. Seasonal flight activity of the ambrosia beetle, *Trypodendron lineatum* (Oliv.), for 1959 near Parksville, B.C. *Proc. Ent. Soc.* of *B.C.* 57: 30-33.

Chapman, J. A. and J. M. Kinghorn. 1955. Window flight traps for insects. *Can. Ent.* 87: 46-47.

Chapman, J. A. and J. M. Kinghorn. 1958. Studies of flight and attack activity of the ambrosia beetle, *Trypodendron lineatum* (Oliv.), and other scolytids. *Can. Ent.* 90: 362-372.

Fye, R. E., W. W. McMillian, R. L. Walker and A. R. Hopkins. 1959. Distance into woods along a cotton field at which the boll weevil hibernates. *J. Econ. Ent.* 52: 310-312.

Graham, K. 1959. Release by flight exercise of a chemotropic response from photopositive domination in a scolytid beetle. *Nature* 184: 283-284.

Hadorn, C. 1933. Recherches sur la morphologie, les stades évolutifs et l'hivernage du bostryche liseré (*Xyloterus lineatus Oliv.*). Suppl. aux. org. de la Soc. forest. Suisse No. 11. Buchler and Co., Bern.

Kinghorn, J. M. and J. A. Chapman. 1959. The overwintering of the ambrosia beetle *Trypodendron lineatum* (Oliv.). *Forest Sci.* 5: 81-92.

Kinghorn, J. M. and E. D. A. Dyer. 1960. Overwintering of ambrosia beetle. *Canada Dept. Agr. For. Biol. Bi-monthly Prog. Rept.* 16(1): 4.

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## Tests of the Nematode DD 136 and an Associated Bacterium for Control of the Colorado Potato Beetle, *Leptinotarsa decemlineata* (Say)

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Extensive trials showed that a nematode of the family Neoaplectanidae and its associated bacterium did not act as a permanent or temporary biological control agent against the Colorado potato beetle, *Leptinotarsa decemlineata* (Say). These trials and the causes of the failure were investigated for a number of years at Belleville; the initial test was reported by Welch (1958). The nematode, commonly known as DD 136, was discovered in codling moth larvae by Dutky and Hough (1955). It is ingested with food by the host, passes through the gut wall into the haemocoele, and releases a bacterium that multiplies rapidly and kills the host. The nematode feeds on the body contents of the dead host, passes through several generations, and eventually leaves the host as an

infective larva. Dutky, and we, found that many kinds of insects can be infected by the nematode in the laboratory. It may be reared in large numbers by infecting larvae of the greater wax moth, *Galleria mellonella* (L.). The larvae die within 36 hours at room temperature and are then placed on wet filter papers in a trap designed to recover the nematodes that emerge from the dead hosts. Storage of the nematodes in water at 45° F. for a month or more causes no decrease in vitality or infectivity, so that large numbers may be accumulated for field trials. These sturdy animals may be applied with a mechanical sprayer at pressures of 100 psi without injury.

This investigation on a pest of a loose-leafed herb is part of a study in which the nematode was tested against common pests in six niches: the root, the tight-leafed herb, the loose-leafed herb, the cereal, the tree, and the aquatic environment. With data obtained from these studies it should be possible to predict the possible value of the nematode against insects of similar or related niches. Three of these projects are well advanced and are reported elsewhere (Welch and Briand, 1961).

All field experiments were done at the Institute's Field Station, ten miles north of Belleville at Chatterton, Ontario, during the summers of 1957-1960. Latin square designs were used in the field trials. Planting and cultivation of the potatoes were done by Mr. Allan Dempsey, the Institute's Horticulturist.

### Laboratory Studies

Various tests were designed to show the nature and symptoms of infection and the time that would be required for onset of mortality in the field. Small lots of potato beetle larvae of each instar, reared from eggs laid in the laboratory by overwintering adults were fed fresh potato leaves inoculated with infective larval nematodes and held at several temperatures. Active beetle larvae soon became infected, stopped feeding, remained inactive, dropped from the leaves and died within 36-48 hours at room temperature. Before death the beetle larvae became dark brown in colour, flaccid to the touch, and were still of the same colour with little putrefaction even five days after death when the cadaver contained adults and multitudes of larval nematodes.

The onset of mortality was related to temperature. Median effective times for mortality at 65° and 75° F. were, respectively: 1st Instar, 70 and 34 hours; 2nd Instar, 53 and 29 hours; 3rd Instar, 63 and 37 hours; and 4th Instar, 52 and 35 hours. Such a range of values for each temperature may be attributed to variations in dosage caused by the application technique of inoculating potato leaves. Nevertheless, the data are useful inasmuch as the technique resembles the process of natural infection in the field. As the mean daily temperature for July in this region is 65° F., the data indicate that dead larvae might be expected in the field as early as 52 hours after spraying.

While the obvious time to apply the nematode against the potato beetle is during the actively feeding larval period, it is possible that mature larvae, burrowing into the soil to pupate, could be infected. Laboratory tests at three dosage levels in small metal tins containing soil produced infected larvae: 36 per cent at the rate of 32 nematodes per cc. of soil, 17 per cent at 59 nematodes per cc., and 60 per cent at 115 nematodes per cc. These data indicate that the prepupal stage can be infected, but a calculation based on the 60 per cent mortality reveals that about $3 \times 10^7$ nematodes would be required to produce a similar density in the soil for a depth of 10 cm. sufficient to infect prepupae that drop within a 30 cm. radius of the plant stem.

TABLE I
Mean number of potato beetle larvae before and after treatment

| Year | | Untreated | Treatments Nematode concentration per ml. | | | | DDT |
|---|---|---|---|---|---|---|---|
| | | | 500 | 1000 | 2000 | 4000 | |
| 1957 | Before | 41 | — | 61 | — | — | — |
| | After | 33 | — | 39 | — | — | — |
| 1958 (I) | Before | 55 | 54 | 82 | 59 | — | 64 |
| | After | 56 | 63 | 51 | 56 | — | 2 |
| 1958 (II) | Before | 18 | 20 | 24 | 20 | — | 22 |
| | After | 11 | 10 | 16 | 16 | — | 0.1 |
| 1959 | Before | 33 | — | — | 44 | 38 | 52 |
| | After | 34 | — | — | 38 | 36 | 0.2 |

**Field Studies**

The nematode treatments, the check, and the DDT applications were made on potatoes planted in rectangular plots of not less than 25 plants each. Treatments were made in early July when the potato beetle occurred mainly as third- and fourth-instar larva. The nematodes were applied with a mechanical sprayer at the volume of 100 ml. per plant in four concentrations, 500, 1000, 2000, and 4000 nematodes per ml. The number of nematodes per square centimetre of leaf was determined by washing leaf samples, determining leaf area, and counting the recovered nematodes. For the above concentrations the leaf dosage averaged respectively 5, 9, 18, and 36 nematodes per square centimetre. The leaf measurements also revealed that the nematodes were evenly distributed in the plot, and that the highest dosage occurred on the upper leaves of each plant. Samples of nematodes were taken from the sprayer nozzle and brought into the laboratory to check the nematode concentration, and infectivity against wax moth larvae; all infectivity tests were positive. Beetle mortality was measured indirectly by determining the change in the number of larvae on randomly chosen plants before and after treatments, and directly by recovering the dead larvae on wooden trays set below the foliage.

While the first trial in 1957 gave a statistically significant reduction in the population of the beetle larvae (Welch, 1958), trials in 1958 and 1959 did not verify the 1957 findings, but showed only small reductions in numbers that were not statistically significant.

Table I shows the mean number of beetle larvae per plant before and after treatments. Each mean in 1957 was based on 54 plants, in 1958 on 35 (7 plants per plot), and in 1959 on 36 (9 per plot). The field trials in 1958 (I) and 1959 generally showed a greater decrease in the nematode-treated plots than in the untreated plots. Analysis of variance revealed that heterogeneity existed in the population counts, but even where this was removed by conversion to random block designs, the differences were not statistically significant.

Though the plot data gave gross effects, it is possible that the changes in counts on individual plants might be related to the level of nematode dosage or to the initial numbers of beetles. Accordingly, the ratio of the beetle counts on each plant before and after treatments were plotted against initial beetle counts, and against nematode dosage per square centimetre of leaf. These latter measurements were taken on most of the plants used for beetle counts. Though trends were apparent, the points were scattered, and the regression coefficients not statistically significant.

**On the Failure of the Nematode to Infect the Beetle**

The actual causes of the failure of the nematode and its bacterium to produce control of some practical value cannot be positively determined but circumstantial evidence suggested that the failure was not attributable to the nematode and its bacterium, but to the environment in which they were used.

Nematodes were sprayed in water droplets, and, as nematodes require moisture for survival and activity, the rate of droplet evaporation and drying of leaves is critical. Relative humidity and air movement govern drying rates. An examination of the microclimates of the potato plots during the spraying and for eight hours afterwards showed that the nematodes were effective when humidities were high both during and after spraying. Laboratory observations on the drying time of water droplets (0.8 $\pm$ 0.03 mm. in diameter) on exposed leaf surfaces revealed that at 80° F. and at humidities of 40, 50, 60, and 70 per cent half of the droplets had evaporated at 9.5, 11, 16, and 19 minutes respectively. At 80 and 90 per cent humidities the 50 per cent drying times under the above conditions were estimated to be 26 minutes and 38 minutes respectively. These determinations were made in air moving at rates of 4 miles per hour. With an increase or decrease of one mile per hour in air speed, the evaporation time increased or decreased by 10 to 15 per cent. Using these and the temperature and humidity data from the three summers, we were able to determine that the nematodes survived at least one hour in 1957, but were probably dead in 15 minutes in 1958, and in 30 minutes in 1959. These figures suggest why the field mortality of beetle larvae was significant in 1957, and insignificant in 1958 and 1959.

A number of field tests were made of the effect of increased humidity on beetle mortality. Verification was obtained in a small plot covered with a plastic tent. Humidity remained above 90 per cent in this plot, while in an uncovered plot it varied from 40 to 85 per cent. The number of beetles in the covered plot dropped from 54 to 11 per plant, while the control decreased from 53 to 48. Spraying after sunset, excessive sprinkling of the plots by water before treatment and close planting of potatoes to benefit from their mass effect in stabilizing and increasing ambient humidity, produced similar but less dramatic demonstrations of the importance of humidity to beetle infection.

Another approach to the drying problem was the addition of chemicals to the water carrier to retard droplet evaporation. Glycerine, honey, glucose, sorbitol, urea, and agar were tested and found effective in retarding water evaporation only at high concentrations. At high concentrations the chemicals are often nematocidal, or may cause harm to the plants. Glycerine caused yellow spotting, whereas sugar and honey solutions encourage fungal diseases.

The manipulation of nematode concentration provides another means of overcoming the effect of drying on nematode survival and infection of beetle larvae. Unfortunately the field data gave no indication of the levels necessary for significant beetle mortality. Deductions were made from laboratory experiments and from a dosage-mortality experiment to determine the nematode application per plant necessary for significant mortality under near ideal conditions. In the laboratory active third- and fourth-instar larvae consumed 0.3-0.4 square cm. of leaf per hour per individual (Welch and Kaye *in prep.*). One nematode could parasitize and introduce sufficient bacteria to kill a host, but in nature the number is probably greater: feeding experiments showed that starved beetles did not become infected unless the small piece of leaf that they consumed held four or more nematodes. Thus, if a larva was to consume within an hour the four or more nematodes necessary for infection, there must be 10-12

nematodes on each square centimetre of leaf (comparable to a field concentration of 1000-1200 per ml.). If the humidity is low, then survival time would be less, and the concentration proportionately higher.

More reliable data were obtained from a dosage-mortality experiment in a glasshouse. Flowering potato plants were sprayed with nematodes to give leaf dosages of four to 186 nematodes per square cm. (no. per sq. cm. equalled one twenty-second of nematode concentration in ml.). The test was at humidities greater than 80 per cent, with no air movement and at 80° F. The median lethal dose was about eight nematodes per sq. cm., comparable to a field concentration of 900 per ml. or an application of 90,000 per plant. These and the previous figures indicate that under ideal conditions the nematode field application should exceed 90,000 per plant for 50 per cent mortality, and be at least 300,000 per plant for more than 80 per cent mortality.

Ideal conditions would involve relative humidities in excess of 80 per cent, little air movement, a nematode dosage exceeding 100,000 nematodes per plant, and a temperature range of 70° to 80° F. These conditions agree with the findings of Chamberlin and Dutky (1958) who obtained 80-85 per cent mortality of tobacco insects when the foliage was wet with rain, the humidity high, and the dosage at approximately 50,000 nematodes per tobacco plant, but no control when the leaves were dry and the humidity low. Though the nematode has potentialities, and the above conditions often occur in temperate and tropical regions, the use of the nematode as a temporary biological control agent against insect pests on exposed plant surfaces such as potato, tomato, and tobacco plants, might be possible where local conditions are propitious, but in general would be impractical. The chances of success for the nematode as a permanent biological control agent seem limited; the only possibility would involve soil infection of prepupal stages, and replanting of the crop in the same area in succeeding years. While the first factor was discussed earlier, the value of the second would be restricted by the limited movement of the nematodes in the soil.

**Summary**

The nematode DD 136 and its associated bacterium failed to act as temporary or permanent biological control agents in a series of field trials against the Colorado potato beetle. Investigations of the causes of failure revealed the need of moisture in the environment for nematode survival and infectivity. Various measures were tested for increasing moisture; namely, water sprinkling, night application, and the use of chemicals to retard evaporation. Nematode dosage levels on plants and the effect of temperature on beetle feeding and nematode infectivity were examined in the laboratory and glasshouse. Ideal conditions were defined, but their absence in Ontario preclude the use of the nematode against the potato beetle in this area.

**References**

Chamberlin, F. S., and S. R. Dutky. 1958. Tests of pathogens for the control of tobacco insects. *J. Econ. Ent.* 51: 560.

Dutky, S. R., and W. S. Hough. 1955. Note on a parasitic nematode from codling moth larvae, *Carpocapsa pomonella* (Lepidoptera, Olethreutidae). *Proc. Ent. Soc. Wash.* 57: 244.

Welch, H. E. 1958. Test of a nematode and its associated bacterium for control of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say). *Ann. Rept. Ent. Soc. Ontario* 88: 53-54.

Welch, H. E., and L. J. Briand. 1961. Field Experiments on the Use of a Nematode for the Control of Vegetable Crop Insects. *Proc. Ent. Soc. Ontario.* In press.

Welch, H. E., and S. Kaye. Amount of leaf consumed by potato beetles at various temperatures. In preparation.

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# A Comparison of the Developmental Rates of One- and Two-Year Cycle Spruce Budworm[1]

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## Introduction

The spruce budworm, *Choristoneura fumiferana* (Clem.), is indigenous to most of the boreal forests in Canada and adjacent Eastern and Western United States. Throughout most of this range the budworm maintains a one-year cycle, overwintering as second instar larvae. In some mountainous areas of Alberta and British Columbia, a form of the budworm has a two-year cycle and overwinters as second instar larvae in the first year and as fourth instar larvae in the second year. The habitat temperatures of these two forms were investigated and related to rates of development in an attempt to discover the environmental factor which maintains the two-year cycle budworm as a distinct form even though it is geographically surrounded by the one-year cycle budworm.

The biology of the two-year cycle budworm was first described by Mathers in 1932 for the Barkerville region of British Columbia, and other ecological studies have been made in the Rocky Mountain National Parks (Shepherd, 1958, 1960).

The life cycles of the one- and two-year cycle budworm are similar until the third instar, that is, in both cases the eggs are laid in late summer and the freshly hatched larvae immediately search for overwintering sites. Here they spin hibernacula and moult to the second instar before going into diapause. In spring they emerge and feed as second and third instars in the developing shoots. Larvae of the one-year cycle form continue feeding and moulting until the sixth instar, pupate, and transform to adults. In the two-year cycle form, the third instar larvae stop feeding and migrate towards the centre of the tree, again searching for overwintering sites. They spin hibernacula, moult to fourth instar, and enter diapause for the remainder of the summer and following winter. This second diapause is the chief difference between the life cycles of the one-and two-year cycle forms. The initiation of the second hibernation is at the beginning of the period which usually offers the best weather for budworm survival and development.

The life cycles of almost all budworm in the two-year cycle area are synchronized so that the adults emerge in the same year. Heavy defoliation occurs only during the even-numbered years when the larvae are in the last two instars; this gives the trees a chance to recover in the alternate years.

At least three distinct populations have been recognized in the spruce budworm complex in Canada: the eastern one-year cycle form, the western one-year cycle form and the western two-year cycle form. A discussion of the relationships of this complex has been presented by Freeman (1958). Stehr (1959) from his studies of gene frequency of a hemolymph polymorphism and also through breeding experiments with these populations, has shown that the eastern and western one-year cycle forms have the greatest differences in their characteristics with the two-year cycle budworm intermediate between the two. This raises the question of the significance of the second diapause in the species complex and the reasons for its continuance in the mountainous areas. Stehr has interbred these populations in the laboratory and has found that there is a slight hybrid inviability with certain specific crosses but not enough to prevent an interchange of genes between the populations.

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TABLE I
Monthly Mean maximum and minimum temperatures for one- and two-year cycle areas of the spruce budworm.

| Area and Year | May | | June | | July | | Aug. | |
|---|---|---|---|---|---|---|---|---|
| | Max. | Min. | Max. | Min. | Max. | Min. | Max. | Min. |
| | One-year cycle areas | | | | | | | |
| Cedar Lake, Ont. 1951 | 62.6 | 40.4 | 66.5 | 47.1 | 72.3 | 51.8 | 66.3 | 50.3 |
| Owl Creek, B.C. 1953 | 67.6 | 39.7 | 68.7 | 49.4 | 79.8 | 48.1 | 77.5 | 50.6 |
| Ft. Norman, N.W.T. 1953 | 54.4 | 33.6 | 65.6 | 43.5 | 72.3 | 48.8 | 68.1 | 47.3 |
| Average | 61.5 | 37.9 | 66.9 | 46.7 | 74.8 | 49.6 | 70.6 | 49.4 |
| | Two-year cycle areas | | | | | | | |
| Marble Canyon, B.C. 1953 | — | — | 56.0 | 36.0 | 66.5 | 37.7 | 66.4 | 40.2 |
| Barkerville, B.C. 1953 | 57.0 | 33.3 | 58.1 | 38.0 | 62.5 | 42.1 | 63.3 | 42.1 |
| Bolean Lake, B.C. 1953 | — | — | 51.3 | 38.4 | 65.9 | 42.9 | 61.4 | 43.4 |
| Average | 57.0 | 33.3 | 55.1 | 37.5 | 65.0 | 40.9 | 63.7 | 41.9 |

The second diapause has been found in small numbers in one-year cycle populations; similarly, individuals have been found in the two-year cycle area which can develop without the second diapause. In fact, some have been found which can develop through to maturity without any larval diapause (Harvey 1957). As there is only an intrinsic difference of three or four days in the total time of development between the one and two-year populations when reared under similar conditions (Stehr, 1953), it can be assumed that the genetic factors responsible for the first and second diapause are present in both the one-year and two-year cycle populations and that some environmental factor has selected and is maintaining the regional differences in diapause characteristics.

**Methods and Results**

Six areas were selected which had histories of spruce budworm outbreaks and which also had reasonably good temperature records. Three of these were from one-year cycle areas, and three were from two-year cycle areas. The monthly means of these areas were calculated from the daily maximum and minimum temperatures and the results appear in Table I. The average temperature difference between all one- and two-year cycle areas for all months was 8.0°F. at the maximum and 7.5° at the minimum. The difference between areas for individual months varied somewhat but the two-year cycle areas were consistently cooler than the one-year cycle areas.

Data on budworm development were available from four of these areas (Fig. 1): Cedar Lake, Ont. (1951), Marble Canyon, B.C. (1952 and 1953), Owl Creek, B.C. (1954), and Ft. Norman, N.W.T. (1959). At each of these locations regular collections were made throughout the season of budworm development with the exception of Marble Canyon where a few of the stages were estimated from field observations, rather than from actual collections. It should be noted that at this location parts of two generations were observed rather than one complete generation. The study began in 1952 when the budworm matured and

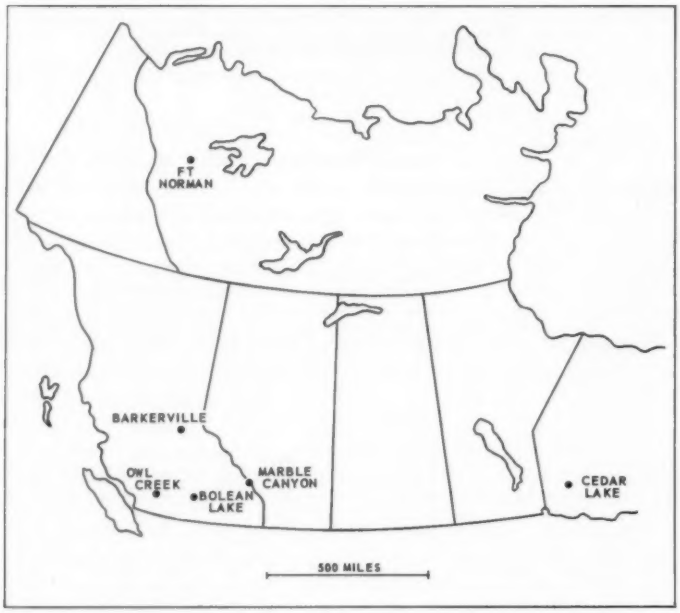


Fig. 1. Location of the areas used in this study. One-year cycle areas: Cedar Lake, Fort Norman, Owl Creek. Two-year cycle areas: Marble Canyon, Barkerville, Bolean Lake.

the data on the early instars were collected the following year. The data from Cedar Lake were complete for the whole life cycle, and those from Owl Creek were complete up to the emergence of adults. Data from Ft. Norman were rather sparse and were not available beyond adult emergence.

The percentage of each developmental stage present in each collection was determined and plotted by date; larvae were segregated into instars by head capsule measurements. From these graphs, curves were drawn showing the percentage of the budworm which had reached each developmental stage or beyond (Fig. 2). The date at which 50 per cent of the insects had reached each developmental stage were determined from these curves and the 50 per cent points for all stages were plotted cumulatively to give a curve of the rate of development for each area (Fig. 3).

The development of the two-year cycle budworm was plotted separately for each year. The material from Ft. Norman was not adequate to separate the third to fifth instars; therefore, a straight line was drawn from the second to sixth instar. Similarly, the date when 50 per cent of the larvae changed from the second to the third instar could not be reliably detected in the Marble Canyon data and a straight line was joined from the second to fourth instars.

The two-year cycle budworm (Marble Canyon) emerges late in the spring and has a slow rate of development. The time required for development of the two-year budworm from the fourth instar to the first instar of the next generation was longer than the time required for the development of the one-year cycle budworm from the second instar to the first instar of the next generation. The northern one-year cycle budworm from Ft. Norman emerges later than budworm from other one-year cycle areas but because of its fast rate of development matures at about the same time.

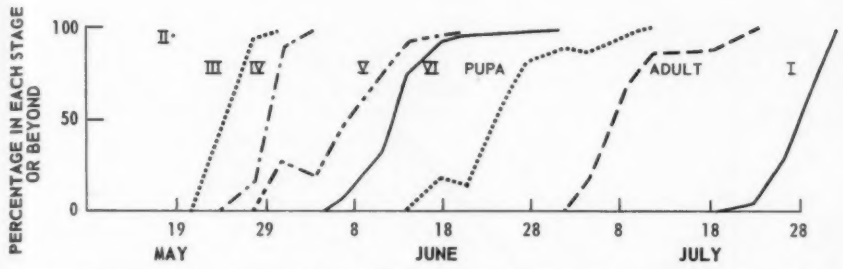


Fig. 2. Percentage of each sample in each developmental stage or beyond; Cedar Lake, 1951.

A comparison of developmental rates was made by plotting the 50 per cent points over the number of days since budworm emergence (Fig. 4). In the two-year cycle material the development was plotted cumulatively after deleting the average time spent in the second diapause. If the two-year cycle budworm were to continue without a second diapause the first instar of the next generation would not be reached until the middle of September. By this time hard frosts are common and it is doubtful if the budworm could persist.

Thermograph charts were available only for Cedar Lake, Fort Norman, and Marble Canyon. The number of degree hours above 42°F. was determined from these charts and plotted cumulatively from the time of emergence (Fig. 5). It is

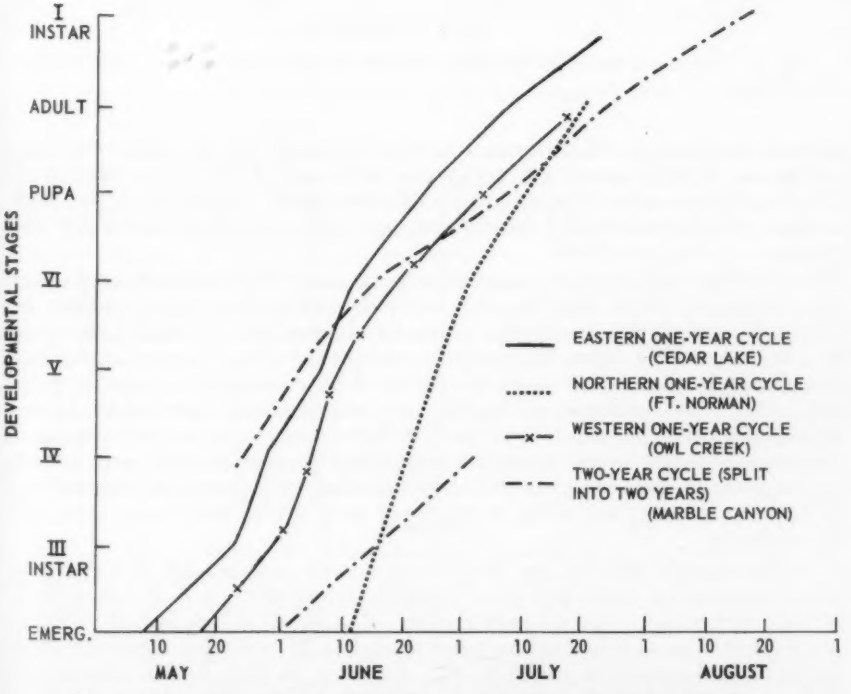


Fig. 3. Date when 50% of the population reached each developmental stage.

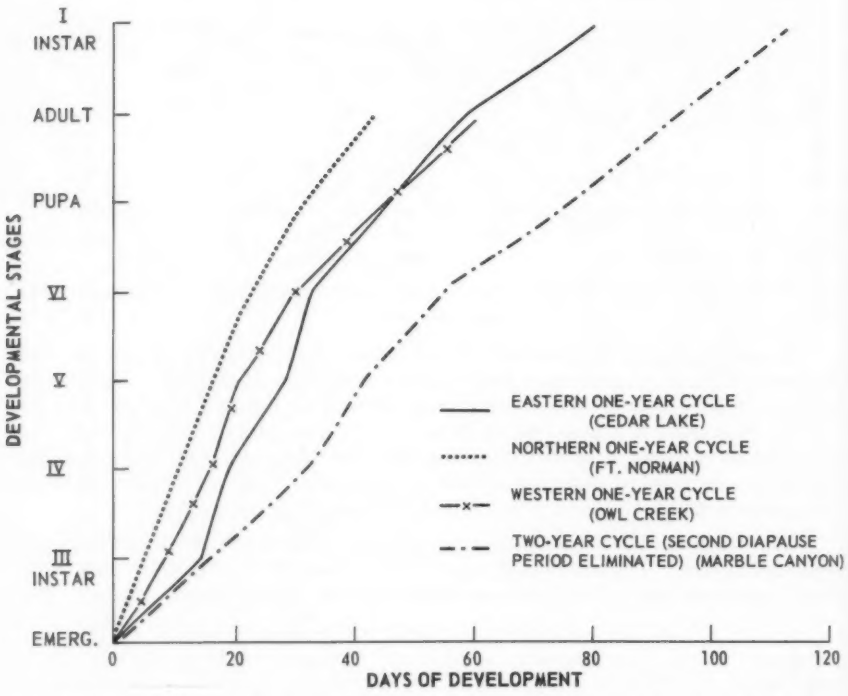


Fig. 4. Time from spring emergence for 50% of the population to reach each developmental stage.

realized that the figure 42°F. is not an absolute threshold and also that the change in the rate of development per degree rise varies considerably over the normal range of temperature. Degree hours, however, gave a measure of the total amount of heat available for development and were considered satisfactory for purposes of this investigation.

The slow rate of development of the budworm in the Rocky Mountain area was attributed to low temperatures. As illustrated in Fig. 5, the number of degree hours was considerably less at Marble Canyon than at Cedar Lake or at Fort Norman. The curves for these latter eastern and northern areas were similar and give little indication of the reason for the faster development of the northern population. Solar radiation can significantly raise budworm temperatures above air temperatures (Shepherd, 1958) and, as the number of hours of sunshine is considerably longer in the north, this factor may account for the faster rate of development in the north than would be indicated by degree hour summations. It may also be an artifact in the technique of using degree hours as an index for development.

The northern area had less diurnal temperature variation and thus the budworm experienced longer periods of moderate temperatures and shorter periods of high temperatures than the eastern form. The differences in diurnal variation are illustrated in a typical thermograph tracing of 24 hours for these two areas and for a two-year cycle area (Fig. 6). To select the days for this illustration, the average number of degree hours per day was calculated for the period from

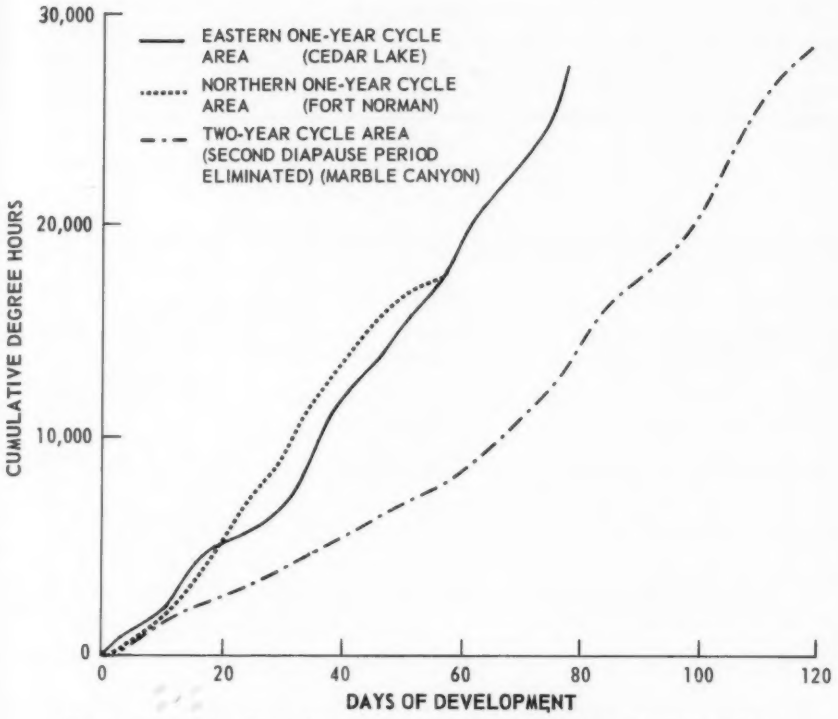


Fig. 5. Cumulative degree hours above 42° F. from beginning of larval activity.

budworm emergence to pupation. A day was selected which came as close as possible to this average figure. The average number of degree hours per day for Cedar Lake was 351, for Norman Wells 320, and for Marble Canyon 174, showing that the average number of degree hours in the two-year cycle areas was approximately half that of the one-year cycle areas.

The temperature data used for area comparisons were for particular years and do not represent average conditions. A table was made of the monthly differences from the long-term means at the closest weather station (Table II) to determine the possibility that the weather differences found were due to unusual weather for these years. In all areas the temperature averages for the period studied were somewhat low, but these averages were relatively lower than normal in the one-year cycle areas than in the two-year cycle areas. This would indicate that in most years the differences between the one- and two-year cycle areas would be even greater than those described here.

## Summary

The one-year cycle spruce budworm occurs in most of the spruce-fir forests across the continent while the two-year cycle budworm predominates at the high altitudes of Alberta and British Columbia. Previous workers have found that all populations contain the diapause factors enabling some budworm to develop with two, one, or no diapause if the proper environmental conditions are present, and further, by means of genetic studies of a hemolymph polymorphism and by breeding studies, have indicated that the two-year cycle budworm is intermediate

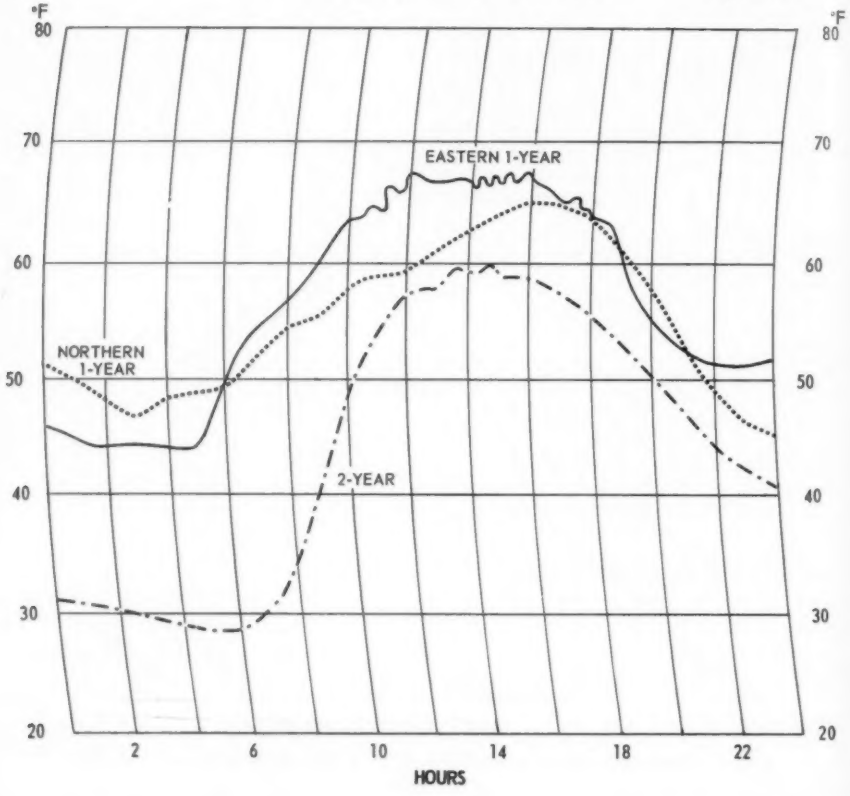


Fig. 6. Representative thermograph tracings for a day with the average number of degree hours above 42° F. between larval emergence and pupation.

in its characteristics between the eastern and western one-year cycle populations. The present studies of habitat temperatures of the two-year cycle budworm correlated with developmental rates of the budworm indicate that in most years the summer season is too short and too cool for the one-year cycle budworm to succeed. This would indicate that cool temperatures during insect development are responsible for the selection and maintenance of populations with a second diapause at the higher elevations of Alberta and B.C.

TABLE II

Differences between average temperatures for the years of study and long-term averages

| | Fort Norman (Norman Wells) | Cedar Lake (Dryden) | Owl Creek (Bralorne) | Marble Canyon (Banff) | |
|---|---|---|---|---|---|
| | 1959 | 1951 | 1954 | 1952 | 1953 |
| May | −5.1 | +3.2 | −1.0 | +0.6 | 0 |
| June | −2.6 | −2.0 | −4.3 | −1.5 | −1.8 |
| July | −1.8 | −2.2 | −4.0 | −1.0 | −0.4 |
| August | −5.2 | −2.5 | −2.7 | −0.6 | +2.2 |
| Average | −3.7 | −0.9 | −3.0 | −0.6 | 0.0 |

**Acknowledgments**

The field data on budworm development and the thermograph sheets were kindly supplied by Mr. A. Rose for Cedar Lake, by Mr. C. E. Brown for Fort Norman, (personal communication), and the data for Owl Creek was extracted from a report by Mr. G. S. Brown, and that for Bolean Lake from thermograph sheets collected by Mr. D. K. Campbell. Members of the Forest Biology Laboratory, Calgary, kindly reviewed the manuscript.

**References**

Brown, G. S. 1956. Studies of the spruce budworm in southern British Columbia. *In* Technical report of the forest insect survey for 1955 Interim report 1955-4, Forest Biology Laboratory, Victoria, B.C.

Freeman, T. N. 1958. The Archipinae of North America (Lepidoptera: Tortricidae). *Can. Ent.* 90, Supplement 7.

Harvey, G. T. 1957. The occurrence and nature of diapause-free development in the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *Can. J. Zool.* 35: 549-572.

Mathers, W. G. 1932. The spruce budworm in British Columbia. *For. Chron.* 8: 154-157.

Rose, A. H. 1952. Investigation of the phenology of forest insects and their host trees. *In* Annual Technical Report, 1951, Forest Insect Laboratory, Sault Ste. Marie, Ontario.

Shepherd, R. F. 1958. Factors controlling the internal temperature of spruce budworm larvae, *Choristoneura fumiferana* (Clem.) *Can. J. Zool.* 36:779-786.

Shepherd, R. F. 1960. Phytosociological and environmental characteristics of outbreak and non-outbreak areas of the two-year cycle spruce budworm, *Choristoneura fumiferana*. *Ecology* 40: 608-620.

Stehr, G. W. K. 1953. Investigations of the genetic structure of forest insect populations. Mim. Ann. Tech. Rpt. 1952, Forest Insect Laboratory, Sault Ste. Marie, Ontario.

Stehr, G. W. K. 1959. Hemolymph polymorphism in a moth and the nature of sex-controlled inheritance. *Evolution* 13: 537-560.

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## Influence of Food on Fecundity and Longevity of Adults of *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae)

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The females of many species of chalcids, braconids, pteromalids, and ichneumonids feed on the body fluids or hemolymph of their host. The fact that the adult males do not partake of this food indicates that such feeding may be associated with egg production. Carbohydrate foods, in addition to the body fluids of the host, are essential to egg production in certain species. Feeding on the host by females of certain hymenopterous parasites increases their value as control agents. This feeding sometimes may be more important than parasitism as a cause of host mortality. *Itoplectis conquisitor* (Say), a host feeding parasite, is considered in this paper.

**Previous Work**

*Itoplectis conquisitor* is a native internal parasite of many lepidopterous pupae in North America. Among the pests of economic importance that it attacks are: *Pieris rapae* L., *Porthetria dispar* L., *Malacosoma americanum* (F.), *M. disstria* Hbn., *Ostrinia nubilalis* (Hbn.), *Rhyacionia buoliana* Schiff., *Carpocapsa pomonella* L., *Hyphantria cunea* (Drury), and *Choristoneura fumiferana* Clem. (Muesebeck *et al.*, 1951). Such a wide variety of potential hosts enables the females of this species to feed in the field or laboratory on host body fluids

of a variety of species. Johnston (1913) observed females feeding at intervals on the body fluids of the host. These fluids were exuded when the ovipositor was "pumped up and down" through the cocoon of the larvae or pupae of the cabbage looper, *Trichoplusia ni* (Hbn.). In field observations (Leius, 1960) females were often observed feeding on the body fluids of *P. rapae* and *R. buoliana* pupae. In the laboratory, females supplied with pupae of the greater wax moth, *Galleria mellonella* (L.), fed on body fluids of this host.

The diet of this species is not limited to host body fluids. Observations in the field (Leius, 1960) showed that the adults of *I. conquisitor* visited a variety of flowering plants, such as *Silene cucubalus* Wibel, *Melilotus officinalis* (L.), *M. alba* Desr., *Medicago sativa* L., *Pastinaca sativa* L., *Daucus carota* L., *Asclepias syriaca* L., and *Convolvulus arvensis* L. Adults, especially males, appeared to prefer umbelliferous plants to other flowering plants. In the spring and autumn when flowering plants were scarce numerous females and males of *I. conquisitor* were seen feeding on the honeydew of *Shizolachnus pini-radiatae* (Davids.), an aphid found on the needles of red pine, *Pinus resinosa* Ait. In the laboratory both males and females often ate diluted honey, sucrose solution, and soaked raisins as substitutes for nectar and other natural foods.

The food of adult hymenopterous parasites includes certain minerals, carbohydrates, proteins as a source of various essential amino acids (Pratt, 1950), sterols and vitamins (Trager, 1953), and water. The adult hymenopterous parasites tested by Doten (1911), Smith (1930), and Györfi (1945), did not live more than a few days in the absence of food and water; water alone slightly increased the average life span. These workers showed that the females of certain hymenopterous parasites may live several weeks or longer when fed on diluted honey or equivalent nutrients.

Feeding on the host is of great importance to the females of many hymenopterous parasites in increasing their fecundity and longevity (Howard, 1910; Rockwood, 1917; Spencer, 1926; Lloyd, 1940). In fact *Exeristes roborator* (F.), *Dibrachoides dynastes* (Foerst.), and *Bracon brevicornis* Wesm. will not oviposit until they have eaten body fluids of the host (Genieys, 1925; Fox, 1927; Smith, 1930). Flanders (1935), however, found that when the female adult of certain pteromalids emerges from the host, the oocytes are in all stages of development and sufficient food is stored up during the larval period to permit the maturation of a few eggs before the parasite emerges. It appears that here the nourishment for continued oviposition is derived from carbohydrate food or the body fluids of the host.

Schneider (1941) showed that egg resorption occurred only when ovulation was inhibited. Flanders (1942) found that in the females of certain pteromalids the occurrence of oosorption prior to ovulation, and the storing of mature eggs after ovulation, are adaptations for maintaining the reproductive capacity of the species when environmental conditions are unfavourable for oviposition; eggs may be stored for periods longer than that necessary for incubation only when they lack nutritive substances necessary for embryonic development. Edwards (1954) found that in *Nasonia vitripennis* (Wlkr.) (Pteromalidae) egg resorption took place when females were fed carbohydrate foods and ceased when body fluid of the host was supplied. Varley and Edwards (1957) found that when the females of *N. vitripennis* were allowed to oviposit on their host they formed a feeding tube through which they obtained body fluids; this protein-rich food accelerated egg maturation and the ovaries soon contained rapidly developing oocytes in addition to mature eggs; by this time the fat bodies had disappeared, and if such females were starved, oosorption was extremely rapid and death oc-

curred in a very short time. If fed carbohydrates only, the females survived, but the total number of eggs in the ovaries slowly decreased. Flanders (1942) found that some non-viable eggs were laid when a female parasite had been deprived of hosts; he suggested that these were eggs in the early stages of resorption but in which the chorion was still sufficiently strong to withstand the passage through the ovipositor.

## Materials and Methods

Immature stages of *Itoplectis conquisitor* were reared in the laboratory on the pupae of the greater wax moth, *G. mellonella*. Adults that emerged on the same day were placed in standard test cages (15" x 8 3/4" x 8 3/4"). The first experiment was conducted at a constant temperature of 72 ± 1°F. and a constant relative humidity of 66 ± 1 per cent. The second experiment was conducted at a constant temperature of 76 ± 1°F. and the same relative humidity as in the first experiment.

The diets tested in the two experiments and the code numbers allocated to each diet are shown in the following table.

| | Code Number | Experiment 1 | | Pupae at 35 days | Experiment 2 | |
|---|---|---|---|---|---|---|
| | | No Pupae | Pupae throughout | | No Pupae | Pupae throughout |
| Water | 7 | *[1] | * | | * | * |
| Sucrose solution | 2 | * | * | * | * | * |
| Diluted honey | 5 | | | | * | * |
| Sucrose solution with diluted honey | 1 | * | * | | | |
| Sucrose solution with raisins | 3 | * | | * | | |
| Sucrose solution with pollen | 4 | | | | * | * |
| Aphids' honeydew | 6 | | | | * | * |

[1]*Indicates the diets used in the experiment.

There were thus nine different diets in the first experiment, and ten in the second.

In each experiment, there were two cages for each diet: in experiment one there were eight females and eight males in each cage, while in experiment two there were ten insects of each sex in each cage.

The honey and sucrose were dissolved in distilled water to give solutions containing 37.5 per cent sugar by dry weight. The raisins were soaked in distilled water for 24 hours before using. The pollen was fed as a one per cent suspension in a 37.5 per cent sucrose solution. The honeydew was supplied by placing potted potato plants infested with the aphid *Aphis nasturtii* (Kalt.) in the cages. All other liquid foods were provided in test cages separately (not mixed) on 3/4-inch lengths of dental cotton. The soaked raisins and wax moth pupae were given in separate containers.

To avoid differences in the nutritive value of the food substances, sufficient supplies of honey, sucrose, raisins, and pollen were obtained to last for the duration of the experiments. The pollen was hand collected from Scots pine, *Pinus sylvestris* L., and air dried before use. Wax moth pupae were reared in the laboratory, and only those that were light brown in colour were used in the experiments. In cages with carbohydrates or vegetable proteins and where the

wax moth pupae were not part of the diet all pupae were covered with a double layer of plastic screen so that the *I. conquisitor* females could not feed on them. In cages where wax moth pupae were part of the diet four pupae were covered with plastic screen and four pupae were exposed in an uncovered shallow glass container. The wax moth pupae and all foods, except honeydew, were renewed daily. To determine the fecundity the wax moth pupae that had been exposed were dissected and the number of eggs deposited each 24 hours recorded. Daily records of *I. conquisitor* mortality were kept. The duration of each experiment was from the time the *I. conquisitor* adults emerged until all insects in the test cages had died. The two experiments were conducted with different insect populations and at different times.

Analyses of variance and Duncan's multiple range test (Duncan, 1955) were applied to examine the significance of the differences between the fecundity and longevity of the adults on different diets. Results were analysed for each sex separately, and estimates of error variance were estimated from differences between duplicate cages.

## Results

The adults of *I. conquisitor* usually did not feed on the day of emergence. Feeding normally started on the second day but only on carbohydrate and vegetable protein foods. In the first experiment, where the temperature was 72 ± 1°F. this type of feeding lasted from 7 to 10 days. After this initial feeding the females punctured the host pupae and fed on the body fluids of the host in addition to the carbohydrates. To obtain more fluid from a pupa, the female, after piercing the cuticle, enlarged the puncture hole with circular movements of the abdomen and ovipositor. When the puncture hole was sufficiently large the female removed her ovipositor and fed on the exuded fluid. There was no evidence that the females of *I. conquisitor* fed on tissues of the host pupae other than exuded fluid. Usually each female punctured and fed on a number of pupae. In a typical test eight females together punctured 12 holes during the first day of pupal feeding, but no eggs were deposited. Twice as many punctures were made the next day and six eggs were deposited. Around the peak of oviposition the pupae were usually covered with punctures; five to six punctures were made for each egg deposited. Thus the females punctured many more pupae for feeding purposes than for oviposition.

In cages where the body fluid of the host was the only source of food some of the females died before they were attracted to the pupae and could feed on the body fluids of the host; but the survivors were able to feed and oviposit on host pupae alone.

In the second experiment, where a higher temperature was maintained the preoviposition period lasted only four to six days. As in the first experiment, puncturing of the host pupae began one day before oviposition, but no mortality occurred in the preoviposition period when host pupae were the only source of food.

### *Influence of Food on Fecundity of the Females of I. conquisitor*

The results of the first experiment showed (Fig. 1-A) that the mean number of eggs deposited per female was greatest for diets containing both wax moth pupae and carbohydrate foods. The few eggs that were laid in cages without host pupae as food could have resulted from stored energy as stated by Flanders (1935) and recently verified for *I. conquisitor* by A. P. Arthur (personal communication). In this experiment the greatest mean number of eggs per female

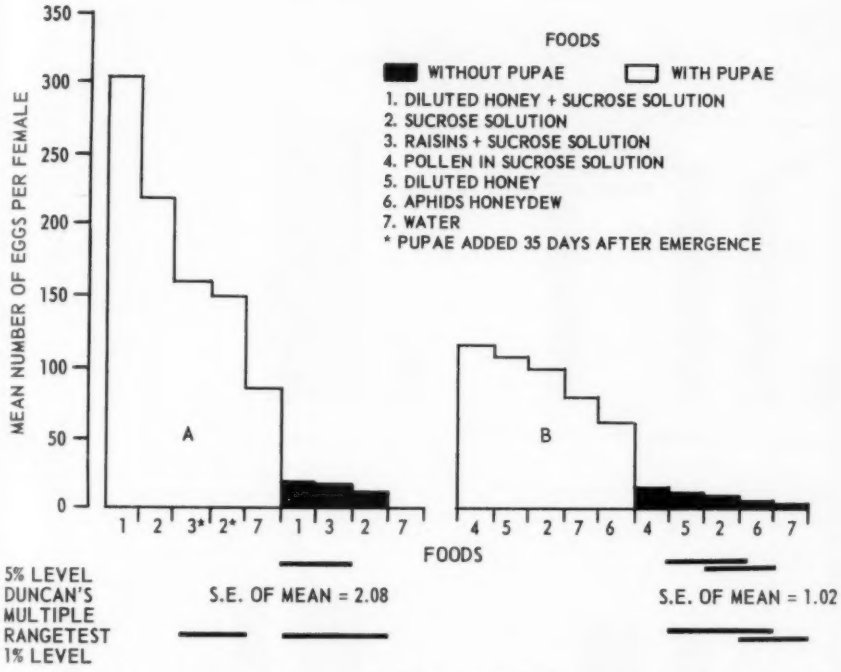


Fig. 1. A comparison of the influence of foods on the fecundity of the females of *Itoplectis conquisitor* in first (A) and second (B) experiment. The means for the foods which are underscored are not significantly different at the 5 per cent (top line) or the 1 per cent (bottom line) level.

was obtained where the females were supplied with diluted honey, sucrose solution, and wax moth pupae. The females that were supplied with sucrose solution, and wax moth pupae deposited fewer eggs, but nevertheless laid more than those females fed on pupae alone. No eggs were deposited where only water was provided.

The effect of the body fluid of the host on the fecundity of the parasite is demonstrated in more detail in Fig. 2, which shows the accumulated number of eggs laid per female, plotted against time, for five of the diets in experiment 1. These five diets afford a comparison of fecundity on diets of carbohydrate (sucrose solution) and carbohydrates with vegetable protein (sucrose solution and raisins), both without pupae and with pupae supplied throughout the experiment (for sucrose solution only) or supplied from 35 days after the emergence of the adult parasite.

The results of the second experiment also showed (Fig. 1-B) that inclusion of host body fluids in the diets significantly increased the mean number of eggs laid by the female. The most effective food for egg production in this experiment was pollen in sucrose solution with wax moth pupae. The females fed on honeydew of aphids and wax moth pupae deposited fewer eggs than those fed on wax moth pupae alone (Fig. 1-B food 6 and 7 with pupae). The mean number of eggs laid per female where wax moth pupae were the only source of food was much less than where the females received, in addition to the pupae, either pollen in sucrose solution, diluted honey, or sucrose solution. Of the diets that

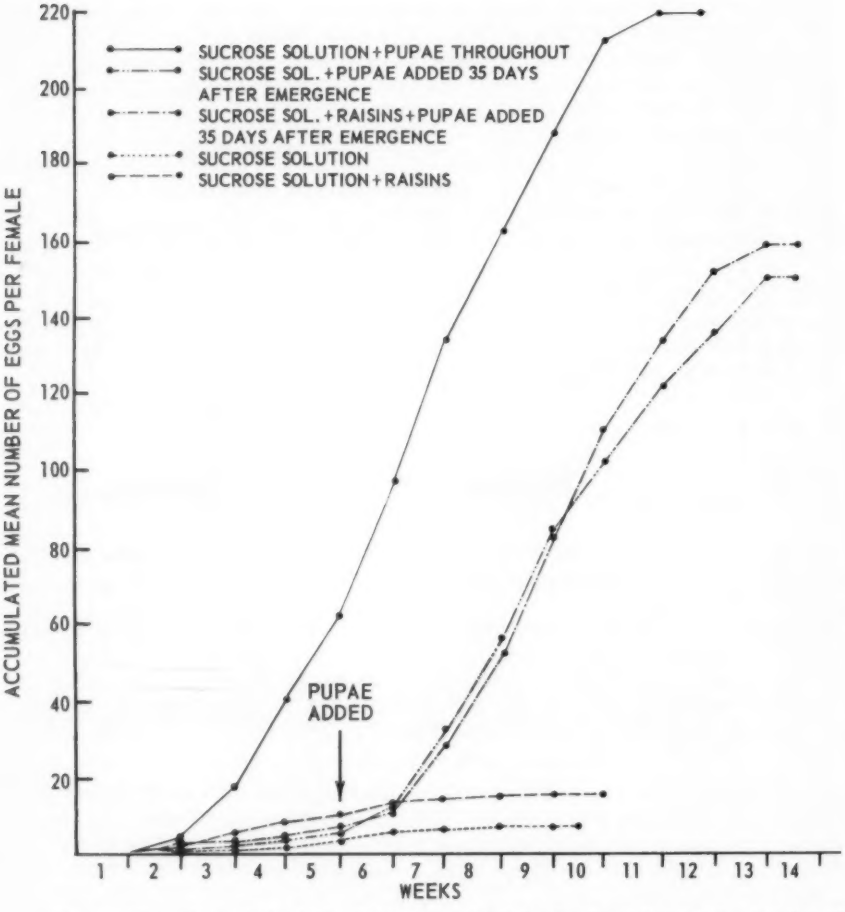


Fig. 2. The effect of the body fluid of the host on the fecundity of the females of *Itoplectis conquisitor*, showing the accumulated number of eggs laid per female, plotted against time, for five of the diets in experiment 1.

lacked pupae, pollen mixed with sucrose solution gave the highest mean number of eggs per female. Diluted honey gave the next highest mean, and was more successful for egg production than was honeydew; sucrose solution gave a mean intermediate to these two, and not significantly different from either ($P<0.05$). The mean number of eggs per female deposited in the test with water alone was less than one, showing that some of the females had not laid any eggs.

There was a good agreement between the results for duplicate cages, in terms of total numbers of eggs laid per female, and this was so for all diets, in spite of the wide differences between mean values for cages on different diets. The greatest difference between duplicate cages was found in the first experiment with a diet of sucrose solution – diluted honey – wax moth pupae, for which the total number of eggs laid per female in the two cages were 311.0 and 303.1.

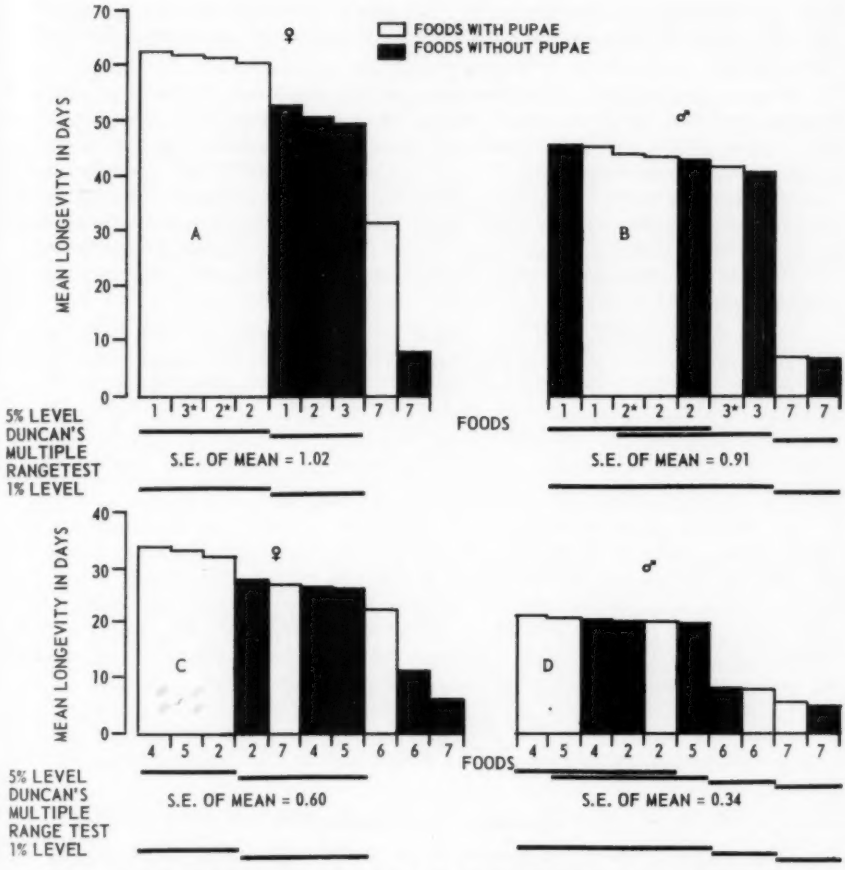


Fig. 3. A comparison of the influence of food on the longevity of the adults of *Itoplectis conquisitor*. The means for the foods which are underscored are not significantly different at the 5 per cent (top line) or the 1 per cent (bottom line) level. A – longevity of females in first experiment, B – longevity of males in first experiment, C – longevity of females in second experiment, D – longevity of males in second experiment. For list of foods see fig. 1.

Before and during the time when oviposition was at its peak the females deposited more eggs in the wax moth pupae under the screen than in the uncovered pupae.

*Influences of Food on Longevity of the Adults*

*Females.*–The first experiment showed (Fig. 3-A) that the females lived longer, under the test condition, when both carbohydrate foods and host pupae were fed. For all the carbohydrate diets with pupae, even those in which the pupae were added 35 days after emergence of the adult parasites, the differences between the mean longevities for the females on the different diets did not reach the 5 per cent level of significance. The mean longevity of females was significantly less where carbohydrate and vegetable protein foods were given without pupae but showed no significant differences between these diets. Pupae alone

were less effective in maintaining life than any of the diets containing carbohydrate or vegetable protein foods alone. On water alone the females lived only 5–11 days.

A second experiment at a different temperature and with different population also showed (Fig. 3-C) that the addition of wax moth pupae to carbohydrate diets significantly prolonged the life of the females (compare Fig. 3-C, foods 2, 4 and 5 with and without pupae). The longevity of females fed on pupae alone was shorter than that of those given carbohydrates in addition to the wax moth pupae. The females kept on water alone had the shortest longevity (individual range 4–9 days). The mean longevity of the females fed on honeydew was significantly less than that of those fed on other foods (Fig. 3-C, food 6 with or without pupae).

*Males.*—The inclusion of host pupae in the diet did not affect the mean longevity of the males in either experiment (Fig. 3-B and D), because they were not attracted to the pupae and were never observed to feed on the body fluids exuding from hosts punctured by females in the same cage. Even when water alone was supplied, and the males lived an average of only 7.2 days in the first experiment or 5.3 days in the second experiment, the addition of host pupae to the diet made no appreciable difference to the longevity.

In the first experiment (Fig. 3-B) the mean longevity of the males fed on diluted honey and sucrose solution was not much greater than the mean longevity of males fed on sucrose solution alone, but it was greater than that of the males fed on raisins and sucrose solution ($P<0.05$). In the second experiment (Fig. 3-D) there were no great differences between the means for the different diets containing carbohydrate foods, although the mean longevity of the males fed on pupae and pollen in sucrose solution was slightly longer than that of the males fed on diluted honey alone. The mean longevity of the males fed on honeydew was significantly less than that found for any of the other foods, except for those males given only water which had an even shorter mean survival period.

## Discussion and Conclusion

The results of these experiments show that the fecundity and longevity of the females of *I. conquisitor* is influenced by their diet. Without body fluids of the host the females deposited very few eggs. The longevity of the females was significantly shorter when fed on diets not containing body fluids of the host. The ability of certain hymenopterous parasites to deposit a few eggs without first feeding on the host is now known to depend on proteins stored during larval development. The present experiments showed that when given only body fluids of the host the fecundity and longevity of the females were significantly lower than that of females given both the host and carbohydrates. This shows that both foods are necessary to increase the fecundity and longevity of the females of *I. conquisitor*. Without food the females did not live long and egg production was practically nil; this is consistent with the results of Edwards (1954) who found that under conditions of starvation the eggs were resorbed and the food contents used for general body metabolism.

Fox (1927) stated that male *Exeristes roborator* (F.), a parasite of the European corn borer ate the "adipose tissue" of the borer, but the amount taken was usually very small. In the present experiments, however, the males of *I. conquisitor* did not feed on the host even when body fluids exuded from hosts punctured by females in the same cage.

Many authors (Györfi 1945 and 1951; Zoebelein, 1956; Lamb, 1959) considered the honeydew of aphids to be an important food for many insects. Zoebelein (1956) recorded 246 species, representing 49 families, that feed on honeydew. Some are obligate feeders on honeydew while others (adults of hymenopterous and dipterous parasites, and also predators such as Coccinellidae, Anthribidae, and Syrphidae) are facultative feeders on honeydew. However, Palmer-Jones *et al.* (1947) and Lamb (1959) showed that honeydew sometimes has undesirable physical properties. Zoebelein (1956) found that different insects produce honeydew of different nutritional values, and that one of the oligosaccharides, namely melezitone, is detrimental to the fecundity and longevity of the honeydew feeders. In the present study, of which the work reported here forms a part, numerous females and males of *I. conquisitor*, and several adults of *Scambus hispae* (Harris) (Hymenoptera: Ichneumonidae) were found in October feeding on honeydew excreted by the aphid, *Schizolachnus pini-radiatae* (Davids.), on red pine needles. In the present experiments when females were fed on diets with or without pupae, those feeding on honeydew of *Aphis nasturtii* (Kalt.) cultured on potted potato plants deposited a lower mean number of eggs per female and had a shorter mean longevity than those fed on other foods, except on water alone. The longevity of the males fed on honeydew was also shorter than for those fed on other diets, except water and pupae, and on water alone.

The present experiments reported here showed that, under the conditions of testing, the greatest fecundity and longest adult life for females of *I. conquisitor* are obtained when not only the body fluids of the host are supplied, but also carbohydrates and pollen as a source of vitamins. This conclusion is consistent with the results of Doten (1911), who studied the relation of food to reproductive activity and longevity in certain hymenopterous parasites, and with those of Shchepetilnikova (1958), who demonstrated the great importance of foods other than the host for the adults of certain parasitic insects.

**Summary**

The females of *Itoplectis conquisitor* usually did not feed on the day of emergence.

The females fed only on carbohydrate and vegetable protein foods during the early part of their preoviposition period.

At the peak of the oviposition period the females punctured the host pupae 5 to 6 times for each egg deposited.

The diet of the females in the oviposition period was not restricted to body fluids of the host. In the present experiments they fed daily on carbohydrate foods.

The greatest reproductive activity and longevity of the females was obtained when they were supplied with carbohydrates as well as body fluids of the host.

Pollen in the diet significantly increased fecundity of the females.

Without the body fluids of the host the females deposited very few eggs.

Females fed on host body fluids alone deposited fewer eggs than those fed on mixed diet (carbohydrates and body fluids of the host), but more than those fed on carbohydrates alone.

Observations showed that the males did not feed on the body fluids of the host. They consumed carbohydrates and vegetable proteins only.

All carbohydrate foods, with the exception of the honeydew of aphids, had similar effect on the longevity of both sexes.

**Acknowledgement**

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**References**

Doten, S. B. 1911. Concerning the relation of food to reproductive activity and longevity in certain hymenopterous parasites. *Univ. Nevada Agr. Exp. Sta., Tech. Bull.* 78: 30 pp.

Duncan, D. B. 1955. Multiple range and multiple F tests. *Biometrics* 11: 1-42.

Edwards, R. L. 1954. The effect of diet on egg maturation and resorption in *Mormoniella vitripennis* (Hymenoptera, Pteromalidae). *Quart. J. Micr. Sci.* 95: 459-468.

Flanders, S. E. 1935. An apparent correlation between the feeding habits of certain pteromalids and the condition of their ovarian follicles. *Ann. Ent. Soc. America* 28: 438-444.

Flanders, S. E. 1942. Oösorption and ovulation in relation to oviposition in the parasitic Hymenoptera. *Ann. Ent. Soc. America* 35: 251-266.

Fox, J. H. 1927. The life history of *Exeristes roborator* F., a parasite of the European corn borer. *Canada Natl. Res. Counc. Report* 21, 1927, 58 pp.

Genieys, P. 1925. *Habrobracon brevicornis* Wesm. *Ann. Ent. Soc. America* 18: 143-202.

Györfi, T. 1945. Beobachtungen über die Ernährung der Schlupfwespenimagos. *Erdeszeti Kiserletek*, Sopron, Hungary, 45: 100-112.

Györfi, T. 1951. Die Schlupfwespen und der Unterwuchs des Waldes. Z. *angew. Ent.* 33: 32-46.

Howard, L. O. 1910. On the habit with certain Chalcidoidea of feeding at puncture holes made by the ovipositor. *J. Econ. Ent.* 3: 257-260.

Johnston, F. A. 1913. On the feeding habits of *Pimpla* (*Itoplectis*) *conquisitor* Say. *J. Econ. Ent.* 6: 144-147.

Lamb, K. P. 1959. Composition of the honeydew of the aphid *Brevicoryne brassicae* (L.) feeding on swedes (*Brassica napobrassica* DC.). *J. Insect Physiol.* 3: 1-13.

Leius, K. 1960. Attractiveness of different foods and flowers to the adults of some hymenopterous parasites. *Canadian Ent.* 92: 369-376.

Lloyd, D. C. 1940. Host selection by hymenopterous parasites of the moth *Plutella maculipennis* Curtis. *Proc. Roy. Soc. London* B, 128: 451-484.

Muesebeck, C. F., Krombein, H. K., and Townes, H. K. 1951. Hymenoptera of America North of Mexico—Synoptic Catalog. United States Dept. Agr., Agr. Monogr. 2, Washington, 1420 pp.

Palmer-Jones, T., Sutherland, M. D., Paterson, C. R., Harris, W. F., and Filmer, D. W. 1947. A recent outbreak of honey poisoning. *New Zealand J. Sci. Tech.* (A) 29: 107-143.

Pratt, J. J. Jr. 1950. A qualitative analysis of the free amino acids in insect blood. *Ann. Soc. Exp. Biol. and Med.* 78: 69-72.

Rockwood, L. P. 1917. An aphis parasite feeding at puncture holes made by the ovipositor. *J. Econ. Ent.* 10: 415-416.

Shchepetilnikova, V. A. 1958. Results of the study on use of parasites and predators in insect control in the Soviet Union. *Trans. Ist Intern. Conf. Insect Pathol. and Biol. Control, Praha*, 1958: 441-453 (in Russian).

Schneider, B. A. 1941. The nutritional requirements of *Tribolium confusum*. Survival of adult beetles on patent flour and complete starvation diets. *Biol. Bull.* 80: 208-227.

Smith, H. D. 1930. The bionomics of *Dibrachoides dynastes* Foerst., a parasite of the alfalfa weevil. *Ann. Ent. Soc. America* 23: 577-593.

Spencer, H. 1926. Biology of the parasites and hyperparasites of aphids. *Ann. Ent. Soc. America* 19: 119-151.

Trager, W. 1953. Nutrition. *In* Insect Physiology, ed. by K. D. Roeder, pp. 350-386. John Wiley & Sons, Inc., New York, N.Y.

Varley, G. C., and Edwards, R. L. 1957. The bearing of parasites behaviour on the dynamics of insect host and parasite populations. *J. Anim. Ecol.* 26: 471-477.

Zoebelein, G. 1956. Der Honigtau als Nahrung der Insekten II. Z. *angew. Ent.* 39: 129-167.

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# Studies on Female Sarcophagid Flies: I. *Sarcophaga aldrichi* Parker, *hinei* Aldrich, *houghi* Aldrich, and *Agria affinis* (Fallén)

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## Morphology of the Genital Segments in the Sarcophagidae

The abdomen, as in other muscoid flies, is composed of a preabdomen of five pregenital segments, of which terga 1 and 2 are fused, thus giving the appearance of four segments. Sterna 1-7 or 1-8 form a relatively narrow chain of ventral segments (Fig. 11). The postabdomen, or genital segments, comprise segments 6-10, some of which are reduced, absent, or modified in other ways. The postabdomen of the Sarcophagidae and Tachinidae usually is "fixed" (not retractable), whereas in the Muscidae and Calliphoridae it commonly is in the form of a retractable ovipositor, which is narrow and elongated when extended but in repose telescoped within the abdomen.

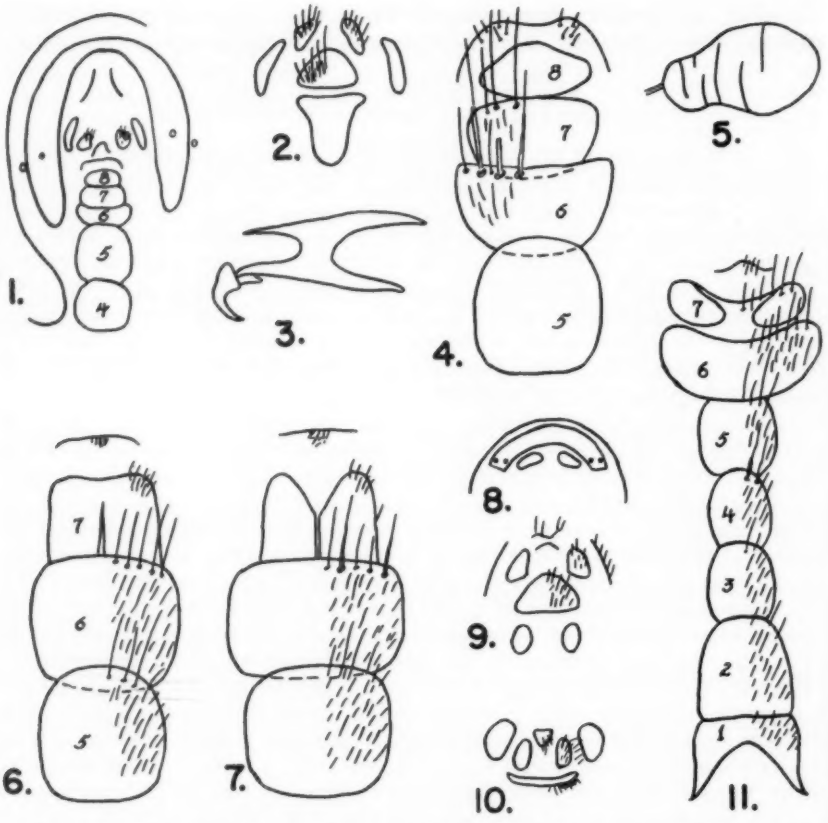
The sarcophagid female genital segments are illustrated in Fig. 1. Tergum 6, the "first genital tergum," is a well-developed sclerotized structure of diverse form, but commonly in the inverted U-shape shown, and bears the seventh (last) abdominal spiracle and sometimes the sixth as well (Fig. 8); terga 8 and 9 are often lacking but one or both of them may be present as smaller sclerotized bands or paired lateral pieces (Figs. 8, 10); tergum 10 often is represented only by the cerci but is sclerotized in *Agria* (Fig. 10). Sterna 6-8, sometimes called the "sternotheca," are often of great importance taxonomically because they display great diversity of form, being at times extraordinarily broadened or narrowed, separated or more or less fused together to form a common plate, often varying in surface sculpture or bristling and sometimes modified to form a piercing larvipósitor. Their usefulness as a taxonomic tool has already been demonstrated in the *Chaetoravinia* complex (Dodge, 1956). Sternum 8 is at times completely unsclerotized (Figs. 6, 7); sternum 9 is represented by the uterus (bursa copulatrix), which sometimes bears a sclerotized plate or plates in its roof (Figs. 2, 9); sternum 10 is a small, setulose, triangular plate (Fig. 2) above which is the anus, which lies between and below the cerci. The unsclerotized anus and vagina are not shown in the figures.

## Notes on the Species
## *Sarcophaga hinei* Aldrich

Figs. 1-5

A female *hinei* was selected to describe and illustrate more fully than the others. The specimen was from a series of 10 males and females collected by Mr. V. Kohler on Pelee Island, Ontario, July 14, 1950. The genital segments are illustrated from an abdomen soaked overnight in a 10 per cent solution of KOH (Fig. 1). The first genital tergum appears as an inverted U-shaped sclerite which is constricted but not weakened, folded or divided mid-dorsally. Spiracle 6 is at the margin of this sclerite; spiracle 7 at the middle of its length. The second genital tergum is absent and the third (tergum 9) is reduced to a pair of elongate sclerites on either side of the cerci, which in turn are dorsal to the tenth sternum (Fig. 2). The anus and vagina (not shown in Fig. 2) lie, respectively, above and below the tenth sternite. Sterna 1-8 are in a chain (sterna 5-8 illustrated, Fig. 4) which, when carefully dissected away, reveals a sclerotized plate in the roof of the uterus. Figure 2 illustrates the tenth sternum

[1]A contribution from the Intermountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Ogden, Utah.




Figs. 1-5. *Sarcophaga hinei.* 1, Posteroventral view of genital segments; 2, Tenth sternum (center) and associated sclerites (sterna 6-8 dissected away), ventral view; 3, Cephalopharyngeal skeleton, first instar larva; 4, Sterna 5 to 8; 5, Spermatheca, much enlarged. Fig. 6. *Sarcophaga aldrichi,* sterna 5-7 (sternum 8 represented by a small patch of spinules). Fig. 7. *Sarcophaga houghi,* sterna 5-7. Figs. 8-11. *Agria affinis.* 8, First and second genital terga, posterodorsal view; 9, Sternum 10 and adjacent sclerites, ventral view; 10, Sternum 10 and adjacent sclerites, posterior view; 11, Sterna 1-7.

and adjacent sclerites in greater detail. Sterna 6-8 transverse, 6 and 7 loosely connected, the sixth slightly broader than 5 and 7 and with three pair of heavy bristles on its posterior margin; sternum 8 with sparse setules and followed by two small groups of setules (Fig. 4). Spermathecae three, ordinary (Fig. 5).

First instar larva: Body with 11 bands of spicules, complete across the dorsum, the last four bands very broad, of about 10 rows of spicules; first seven bands becoming progressively narrower and fainter towards the head end: cephalopharyngeal skeleton as illustrated (Fig. 3).

Range: ONT.: Point Pelee; Pelee Island; Lake Abitibi; ALTA.: Edmonton; Elk Island; WASH.: Seattle; OHIO: Cedar Point, Sandusky (type locality); Put-in-Bay; Lakeside, Catawba Island; Miami County. Records from four Georgia localities by the late Prof. P. W. Fattig (Rabun Bald, Blood Mt., Tray Mt., Blue Ridge) have not been confirmed.

Host: None recorded, but this species is allied to *subaenescens* Aldrich, which was reared from a puparium found in a spider web. It may yet prove to be parasitic on Lepidoptera.

### *Sarcophaga aldrichi* Parker

Fig. 6

First genital tergum setose, pollinose, black, inverted U-shaped, weakened mid-dorsally, with spiracle 6 at hind margin, 7 at middle of length. Sterna 3-5 and 7 of equal width, 6 slightly wider, 8 undeveloped but represented by a small patch of setules at the margin of the vagina (Fig. 5). Sterna 3-5 uniformly setose, sternum 6 with a posterior row of 8-10 stronger bristles, sternum 7 black, brownish apically, subquadrate, flat, with an impressed median longitudinal line, posterior angles setose, posterior margin transverse, faintly emarginate at middle.

Range: Transcontinental in Canada (Arthur and Coppel, 1953); New England; New York; Lake States; ranging south to Santa Catalina Mountains, Arizona, Beulah, New Mexico; and Tray Mt. and Fort Mt., Georgia.

Hosts: The forest tent caterpillar, *Malacosoma disstria*, is its usual host. Rarely recorded from the spruce budworm, *Choristoneura fumiferana;* females taken in Georgia by Harold G. Scott were associated with the elm spanworm, *Ennomos subsignarius*, but its relationship to that insect has not been proved. Arthur and Coppel (1953) also record it from the gypsy moth and the satin moth.

### *Sarcophaga houghi* Aldrich

Fig. 7

Genital segments very much like those of *aldrichi* except that the seventh sternum is deeply notched on its posterior border (Fig. 6); sixth sternum slightly broader than in *aldrichi*.

Range: Mass.; N.Y.; Pa.; Ga.; Stone Mt., Blood Mt.; Kennesaw Mt.; Fort Mt.; Wilscot Gap; Ill.: St. Joseph; Ia.: Traer; Wash.: Shelton; Puyallup; Bothell; Graham Point; Woodinville; Snohomish (unpublished records from Dr. M. T. James); B.C.: Agassiz; Pitt Meadows; Vancouver; Victoria.

Hosts: Knull (1932) reared this insect in Pike County, Pennsylvania, from pupae of the elm spanworm, *Ennomos subsignarius*, and from the fruit tree leaf roller, *Archips argyrospila*. Specimens from Traer, Ia., Fort Mt., Ga., and Wilscot Gap, Ga., are also from *Ennomos subsignarius*. Dr. James' records are from *Malacosoma disstria* and *pluviale;* it is apparently a common parasite of *Malacosoma* in the Puget Sound region. Females from Victoria, B.C., were reared from larvae of *Vanessa antiopa* and *Lambdina* sp., and specimens presumably from B.C. are from *Stilpnotia salicis*.

### *Agria affinis* Fallén

Figs. 8 to 11

Female abdomen flatter, with genital segments more posterior in position than in the preceding *Sarcophagas*, in which these segments are more posteroventral. First genital tergum visible from above, a narrow, crescent-shaped (not U-shaped) sclerotized band with about 18 strong marginal bristles, spiracle 7 above the lowermost bristle and nearly in line with the marginal row, spiracle 6 on the sclerite, near its posterior border (Fig. 8). Second genital tergum a smaller band, divided mid-dorsally, each half with a marginal row of 6-7 bristles; third genital tergum a pair of small plates beside the cerci, each with 5 setules (Fig. 10). Tenth tergum present, triangular, smaller than the cerci (Fig. 10); tenth tergum, cerci and tenth sternum all sclerotized, black in color, setulose. Roof of uterus with two small thickened pigmented spots (Fig. 9, ventral pair),

which seem to lie above the cuticle. Sterna 6-7 transversely broadened, 7 divided into two lateral sclerites, sternum 8 undeveloped, represented by a tuft of setules (Fig. 11).

This species is primarily a parasite of the spruce budworm, the Douglas-fir tussock moth, and other lepidoptera that pupate in foliage. The host is attacked when in the prepupal or pupal stage. Coppel *et al.* (1959) have summarized its host data and its range. Southernmost records for this species are N.M.: Las Vegas Mts. (Aldrich, 1916) and Manzano Mts., Abo (J. U. McGuire).

### Note on the Biologies

It is commonly believed that many parasitic sarcophagids, such as the above three whose biologies are known, are only nominally parasitic species. This belief is strengthened by field observation of parasitized host material, which is quickly reduced to a putrid mass by accompanying bacterial decomposition. The fact that there is no highly refined host-parasite relation such as exists in Tachinidae or the parasitic Hymenoptera does not necessarily prove these species scavengers of even facultative parasites.

In nature these species never have been commonly found except when there is an abundance of a suitable host insect, and at such times it is not unusual to find 60 to 90 per cent of the host cocoons parasitized. It is incorrect to postulate that only weakened, diseased, dead or previously parasitized host pupae are attacked. The writer has removed *S. aldrichi* larvae from cocoons of *M. disstria* before they penetrated the host pupa and found that such pupae will transform to adult moths in a normal fashion.

On the other hand, *Agria affinis* has been successfully colonized in the laboratory on artificial medium by Dr. House, and *S. aldrichi* has been laboratory reared on garbage by Dr. Roger Anderson. Perhaps these species can and occasionally may breed saprophagously in nature, but it has never been demonstrated that they do.

The writer prefers to believe that the wild females have the instinct to larviposit only on suitable fresh lepidopterous host material once the caterpillars have started to spin their cocoons and that, on occasions when larvae may be deposited in offal, their larvae cannot withstand the competition of the more aggressive filth-breeding species.

### Key to the Species

1. Three posterior dorsocentral bristles; abdomen thinly pollinose, subshining ..... 2
   Four posterior dorsocentral bristles; abdomen more strongly dusted with pollen (Sterna 6-7 not much broader than 5, sternum 7 with a median groove, sternum 8 not sclerotized, first genital tergum inverted U-shaped) ..... 3
2. Arista pubescent; no erect median marginal bristles on second apparent tergum; first genital tergum crescent-shaped, broader than deep; sterna 6-7 abruptly broadened ..... *Agria affinis*
   Arista plumose; erect median marginal bristles on second tergum; first genital tergum inverted U-shaped; sternum 8 sclerotized ..... *Sarcophaga binei*
3. Sternum 7 subquadrate, the posterior margin transverse ..... *Sarcophaga aldrichi*
   Sternum 7 with posterior margin deeply notched ..... *Sarcophaga houghi*[2]

### Summary

Females of these four species are keyed and their genital segments illustrated.

The four sarcophagid flies here considered are boreal "blacktailed" species of economic importance because of the parasitic nature of their larvae. Males of all four species were described, keyed and figured by Aldrich (1916) and

[2]The female *houghi* illustrated is from Stone Mt., Ga. Recent dissections of western *houghi* females (British Columbia and Washington) have shown no appreciable difference from the figure for *aldrichi*. More research is indicated to show differences in these two species.

details of the penes figured by Roback (1954). The latter author placed the three *Sarcophaga* in the genus *Arachnidomyia* Townsend. *Agria affinis* was known at that time as *Pseudosarcophaga*, but Coppel *et al.* (1959) have shown that the latter name is antedated by *Agria*.

Collectively, females of this group may be separated from most other sarcophagid species by their entirely black abdomen. The three *Sarcophaga* usually possess a small pair of anterior acrostichal bristles situated just before the transverse mesonotal suture; the *Agria* has several strong pairs of anterior acrostichals. *Sarcophaga pulla* and *aratrix* and the black-tailed species of *Idoneamima* have no anterior acrostichal bristles.

A study of the genital segments has shown that the species of this group may be very readily distinguished specifically. Fresh specimens or museum specimens relaxed overnight in a 100 per cent humidity chamber may be examined by inserting a dissecting needle into the uterus and lifting out the genital sterna, which are often more or less concealed by the tergum. Sometimes it is not necessary to do this, even with dried specimens, for the genital sterna may be sufficiently exposed.

### References

Aldrich, J. M. 1916. *Sarcophaga* and allies in North America. Thomas Say Foundation, Lafayette, Ind., 302 pages, 16 pl.

Arthur, A. P., and H. C. Coppel. 1953. Studies on dipterous parasites of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). I. *Sarcophaga aldrichi* Parker (Diptera: Sarcophagidae). *Can. J. Zool.* 31(3): 374-391, illus.

Coppel, H. C., H. L. House, and M. G. Maw. 1959. Ibid. VII *Agria affinis* (Fall.) (Diptera: Sarcophagidae). *Can. J. Zool.* 37(6): 817-830, illus.

Dodge, H. R. 1956. New North American Sarcophagidae, with some new synonymy (Diptera). *Ann. Ent. Soc. Amer.* 49(2): 182-190, illus.

Knull, J. N. 1932. Observations on three important forest insects. *J. Econ. Ent.* 25(6): 1196-1203, illus.

Roback, S. S. 1954. The evolution and taxonomy of the Sarcophaginae (Diptera, Sarcophagidae). *Ill. Biol. Monog.* 23(3-4): 1-181, 34 plates.

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## The Construction and Performance of a Portable, Precision Spray Chamber

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A spray chamber provides an efficient means for screening promising insecticide compounds, a procedure that oftentimes serves as a useful preliminary to field tests, which are more expensive and less controllable. In research with residual insecticides for controlling bark beetles, we found a need for rapidly reproducing insecticide deposits on sections of fibreboard to test their toxicity. A spray chamber was constructed for this purpose. Its design and operation are described here.

The spray chamber was patterned after one described by Eaton and Secrest (1951) in which the spray is introduced horizontally at one end and allowed to settle onto the test subject. We also relied for a model on a modified version of the Eaton-Secrest spray chamber built by the Forest Service's Lake States Forest Experiment Station, in cooperation with the University of Minnesota (Drooz, 1957).

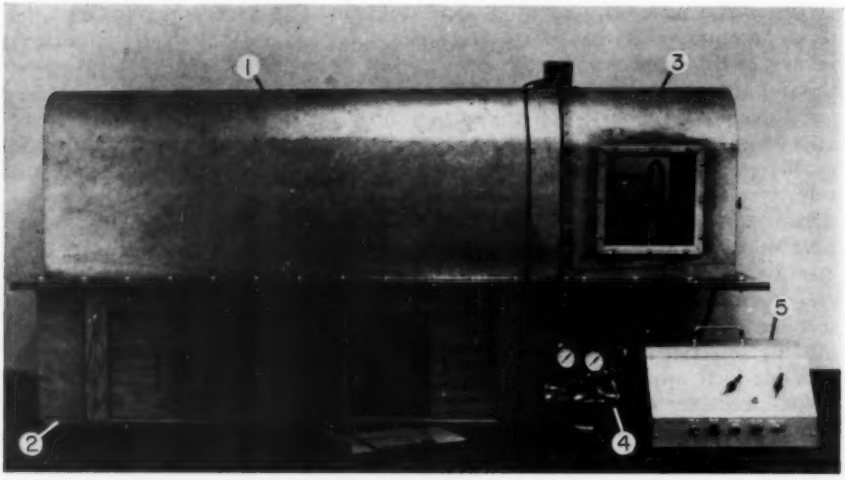


Fig. 1. Spray chamber ready for operation, showing the (1) main chamber; (2) receiving chamber; (3) nozzle compartment; (4) pressure and vacuum pump, and (5) electronic timer.

The spray chamber described here has enough flexibility for use in testing insecticides on most forest insects, and may be used to apply insecticides to the substrate or to the insect directly.

## Spray Chamber Components

The main parts of the spray chamber, including accessory equipment essential to its operation (Fig. 1) are: The spray chamber proper, housing the nozzle, nozzle holder, shutter, and spray reservoir; a pressure and vacuum pump; and an electronic timer.

### *Housing*

The spray chamber housing (Fig. 2) was made so as to be easily disassembled for repair or replacement of parts with ones of special design to fit the needs of different kinds of testing. Metal-to-metal and wood-to-wood surfaces intended to be permanently attached were joined with solder, and water-base glue and doweling, respectively. All sections made to come apart were fastened with bolts or metal screws, and nuts were fixed in place so that the sections can be completely dismantled and assembled with a screwdriver. The housing was constructed mostly from 24-gauge, galvanized sheet metal and ¾-inch, interior plywood. Wooden parts were finished with three coats of a synthetic, plastic varnish, resistant to organic solvents.

The nozzle compartment of the housing holds the nozzle, nozzle holder, and spray reservoir, and protects the operator from errant spray. The top of this unit was rolled into a 12-inch semicircle forming a tunnel-like structure. An end piece was soldered to the front and fitted with a door. A window, sealed with rubber and mounted in a wooden frame, was bolted to each side. The nozzle compartment attaches to the main chamber. The floor of this compartment is formed by a piece of sheet metal which, in turn, rests on the support frame.

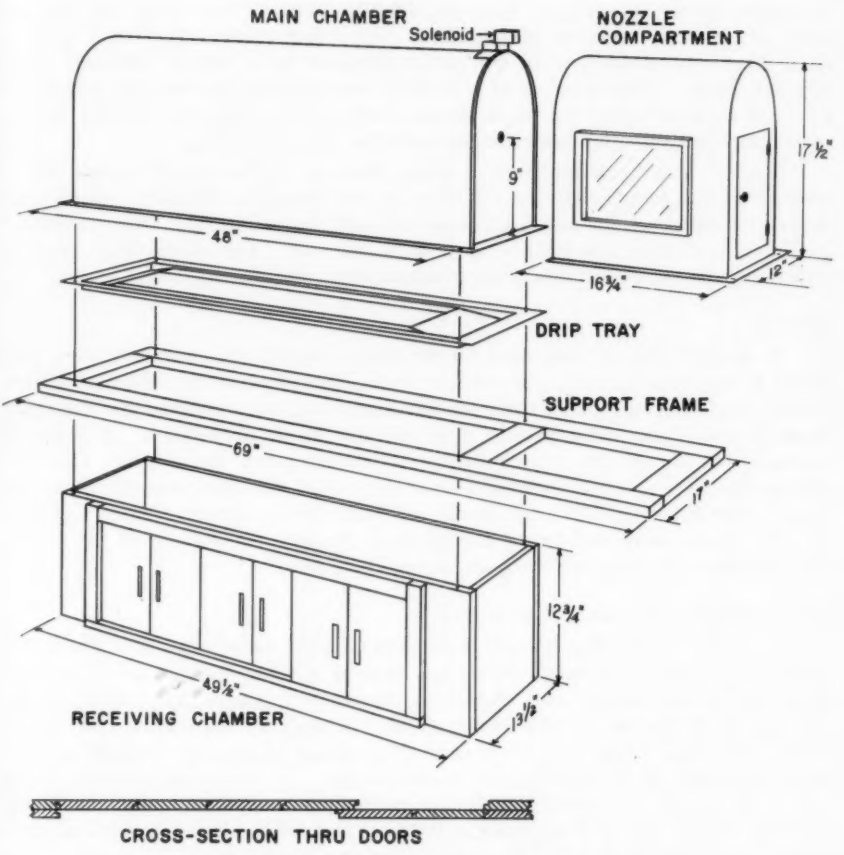


Fig. 2. Diagram of spray chamber.

The main chamber is also tunnel-like in appearance. End pieces are soldered on the front and rear. A door was installed at the rear so the interior could be cleaned. The front has a ½-inch hole through which spray is introduced.

A drip tray forms the bottom of the main chamber and functions as a collector for excess spray that runs off the sides of the main chamber. It prevents the spray from dripping into the receiving chamber and increasing spraying error. Spray falls into the receiving chamber only through an opening, 8 inches wide by 36 inches long, in the drip tray. The drip tray is raised at the edge of its central opening and depressed toward the outside edge so that all spray that impinges on it or flows onto it from the walls of the main chamber runs to a common gutter from which it can be wiped up with cotton or rags.

The main chamber and drip tray rest on the wooden support frame as does the nozzle compartment. These, in turn, seat on the receiving chamber (Fig. 2). The support frame adds strength and rigidity to the housing and serves as a convenient grip when moving it about.

The receiving chamber holds the test objects during treatment. These are introduced through a special set of sliding doors made of plywood, which can

be closed during spraying to keep the deposit pattern from being affected by stray air currents. A cross section of the door construction is shown in Figure 2. Each door was rabbeted to fit the tracks provided for it and to interlock with adjacent doors. The outer set of two doors was designed to close any gap made by (and overlap with) the inner doors at any point along the opening in the receiving chamber. Recessed handles were cut into each door.

Electric power to operate the spray chamber and accessory equipment is centralized in a control box on the front of the receiving chamber. Here four female electrical outlets and a main power switch are located. One outlet has no power and takes the male plug from a solenoid. The other three provide power for the electronic timer, the pressure pump, and for lighting.

*Shutter*

A shutter (Fig. 3) mounted on the front face of the main chamber, just ahead of the spray nozzle, controls the entry of spray into the chamber. The shutter was patterned with little modification after one designed by the Lake States Forest Experiment Station, and was cut from sheet brass. A solenoid mounted on top of the main chamber is used to open the shutter, and two springs close it. A trough is attached to the front of the main chamber under the shutter assembly to collect excess spray that runs off the shutter when it is closed. A plastic hose connected to the trough leads through the bottom of the nozzle compartment, carrying runoff to an outside receptacle.

*Nozzle Holder, Nozzle, and Reservoir*

A nozzle holder (Fig. 4) was devised to hold the nozzle rigidly in place and make it possible to exchange or replace nozzles without greatly disturbing the alignment of the nozzle with respect to the main chamber. Even a slight displacement of the nozzle will bring about a change in delivery. The nozzle holder was made principally of ⅛-inch strap iron. It consists basically of two slide assemblies set at right angles to one another. A turret-like mechanism, to which the nozzle is clamped, is mounted on the uppermost slide. The whole unit rides on two upright rods attached to the floor and ceiling of the nozzle compartment. The right-hand rod is threaded for raising and lowering the nozzle.

Right and left displacements of the nozzle are made by turning the thumb screw on the lower slide assembly. Turning the thumb screw on the upper slide assembly moves the nozzle closer to or farther from the shutter. The turret mechanism rotates the nozzle through horizontal and vertical planes.

An innovation introduced in this spray chamber, compared to the models it was patterned after, is application of the positive displacement principle in the design of the spraying system. In the spray chambers described by Eaton and Secrest and by Drooz[1], flow of the liquid from the reservoir to the nozzle depends upon the siphoning effect of an air blast introduced at the nozzle. In this spray chamber, air pressure is applied directly to the liquid within the insecticide reservoir, and the liquid is atomized by pressure alone as it is emitted from the nozzle. As a result of using this principle, the design of the spraying system is simplified, the range in volume of spray that can be delivered in a unit time is much increased, and the incidental creation of a fine insecticide aerosol that is a hazard to the operator is avoided.

The insecticide reservoir is a tabulated, 500-milliliter vacuum bottle, placed in the nozzle compartment. Pressure is applied on the liquid through rubber

[1]See References.

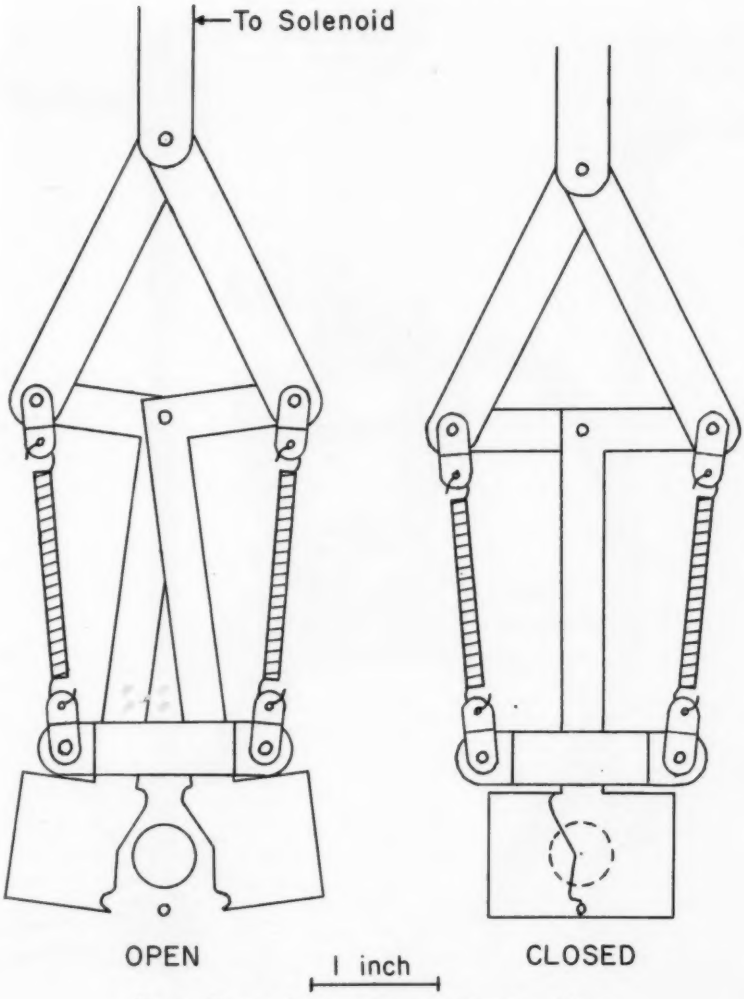


Fig. 3. Shutter shown in open and closed positions.

tubing connected from an air compressor to the tabulation. The mouth of the vacuum bottle is stoppered with a rubber cork. A glass rod extends through the cork to the bottom of the reservoir. The upper end of the rod is connected to the nozzle by rubber tubing.

**Accessory Equipment**

Air pressure is supplied by an electrically driven pressure and vacuum pump (Fig. 1) that is standard equipment and available commercially. The pump has a capacity of 30 pounds/square inch, though 5 pounds/square inch is enough pressure for the liquids we have been working with and is the amount generally used. The compressor rotor is mounted on the motor shaft, making the pump a compact unit. The pump provides a quiet, pulseless air flow, and a given pressure setting will not drift even through interrupted use.

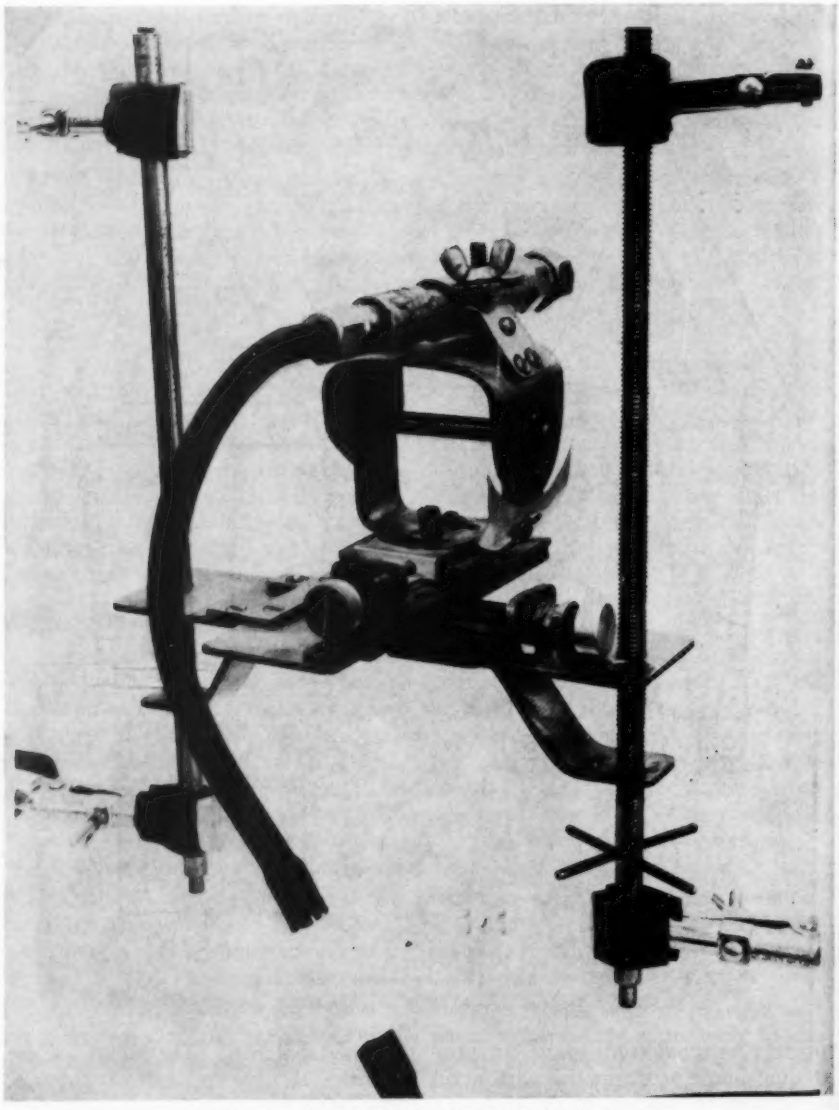

Fig. 4. Nozzle holder with nozzle in place.

An electronic timer (Fig. 1), designed especially for use with the spray chamber, is used to actuate the solenoid. It provides a range in times for opening the shutter from 0.1 to 10.9 seconds in increments of 0.1 second. The shutter, therefore, can be held open for 109 different time intervals, providing a wide range in delivery by the mere expedient of setting dials on the face of the timer. Timer accuracy is unaffected by a drop of as much as 10 per cent in line voltage. The timing device was designed and made by John Dimick of El Cerrito, California, though suitable timing devices are available commercially.

### Operation

Operation of the spray chamber can be simply illustrated by covering the steps of a treatment in sequence. The spray reservoir is filled with the liquid to be tested. The amount of spray in the reservoir has no effect on delivery so it is not necessary to maintain the liquid at a constant level. The timer is set to open the shutter for the desired interval. Two dials on the timer (one in 0.1- and one in 1.0-second intervals) control the total time the shutter will be held open. The timer setting needed to produce a given deposit must be determined by preliminary testing. Test subjects are placed in the receiving chamber on a "carrier" (shown in Figure 1 in front of the open door), and the chamber doors are closed. The carrier provides a convenient grip for moving objects in and out of the receiving chamber and prevents excess spray from being picked up by the objects from the chamber floor. The pump is turned on, forcing spray through the nozzle onto the closed shutter. About five seconds should be allowed to elapse at this point so the tubing and nozzle will fill with spray and assure a smooth-flowing system. The timer switch is thrown. The solenoid pulls the shutter open for the interval shown on the timer dials. When the shutter snaps shut, the pump is turned off and the treated subjects are removed from the receiving chamber. Total spraying time takes between 10 and 15 seconds.

Horizontal distance from the nozzle to the object being sprayed determines the average size of the spray droplets deposited in the receiving chamber. Large drops are propelled farther than small ones, so deposits of larger average drop size are produced as the distance from the nozzle is increased. It is possible, therefore, to study the effect of drop size on the performance of insecticide sprays. Deposits may be sampled anywhere from 6 to 42 inches from the nozzle. All data in this paper were obtained from deposits whose midpoint lay a horizontal distance of 12 inches from the nozzle.

### Calibration and Performance

Spray delivery[2] in the receiving chamber, under uniform environmental conditions, is controlled largely by (1) nozzle orifice, (2) liquid pressure, and (3) shutter opening time. Manipulation of the shutter is the most convenient and accurate way of adjusting delivery over a wide range and in small increments. Changing the nozzle or pressure give only coarse control. Because of this, and because it is inconvenient to adjust the deposit by changing the nozzle or pressure, all calibration was done using the same nozzle, a No. 20 Monarch producing a fan-shaped spray. Most studies were done using a pressure of 5 pounds/square inch.

Calibration was done with kerosene and DuPont oil red dye, using a solution containing 100 milligrams of dye in 1,000 milliliters of kerosene. Delivery was gauged by analysing the dye solution sprayed on 6- by 6-inch aluminum plates placed in the receiving chamber. Five plates were sprayed individually for a given test of delivery. The deposited solution was washed from the plates and assayed colorimetrically with a Duboscq-type colorimeter.

With a No. 20 nozzle, a liquid pressure of 5 pounds/square inch, and a shutter opening of 1 second, delivery was about 7.50 gallons/acre at 70 degrees F. Since the shutter can be held open for from 0.1 to 10.9 seconds in increments of 0.1 second, a deposit of from about 0.75 to 81.75 gallons/acre, in increments of 0.75 gallons/acre, can be produced with liquids similar to kerosene merely by

[2]Delivery is used here to mean the amount of spray deposited on some unit area in the receiving chamber. It does not refer to the output of the nozzle which is termed flow rate.

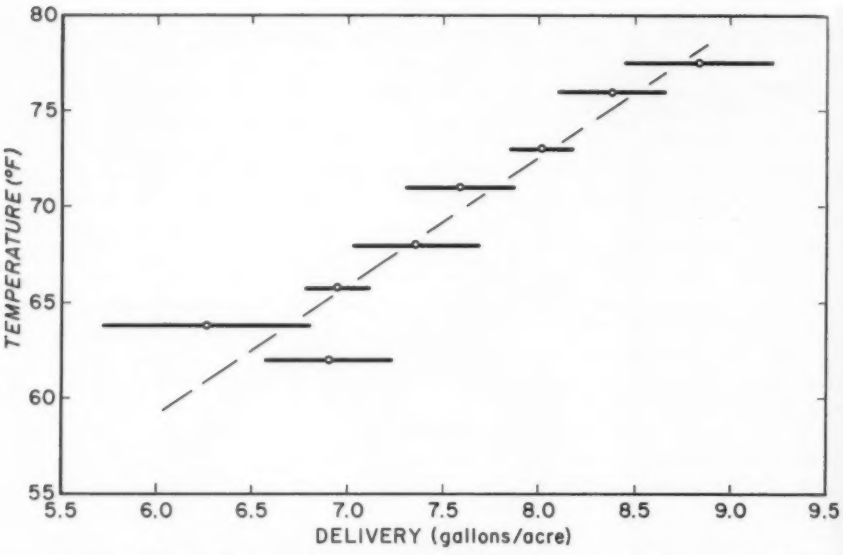


Fig. 5. The effect of ambient temperature on delivery-mean and 95 per cent confidence limits.

turning dials on the timer. This range in the deposit probably includes most levels likely to be used in experiments with the spray chamber. For deposits less than or greater than 0.75 to 81.75 gallons/acre, nozzles of different size can be substituted. Sprays of different viscosity can be expected to give different values than those cited above.

The precision of the spray chamber is shown by the small variation in deposit for a number of different trials; standard deviations ranged from 1.1 to 11.0 per cent and averaged 3.5 per cent (Table I). Ninety-seven per cent of the trials had a standard deviation of less than 8.0 per cent. The standard error within trials ranged from 0.5 to 4.9 per cent and averaged 1.5 per cent. The 95 per cent confidence limits for average gallons/acre ranged from 1.3 to 13.9 per cent and averaged 4.3 per cent. More recent experience with the spray chamber indicates that error will be higher when emulsions are used in place of solutions.

Variation between trials is shown by test numbers 1 through 12, 15, and 19 through 28 (Table I), which were carried out with the same air pressure, shutter opening, and nozzle. Here the deposit varied from 6.26 to 9.57 gallons/acre. The great bulk of this between-trial variation was due to fluctuations in temperature which influence the viscosity of the spray and the size of the nozzle orifice. Evidence for the predominating influence of temperature is given in Fig. 5, which shows the results of trials[3] made as the ambient temperature in the laboratory rose from 62 to 78 degrees F. A line drawn by eye shows that a 20-degree change in temperature produced a 3-gallon change in delivery, amounting to 0.15 gallons/acre for each 1 degree F. Reproducibility is thus strongly affected by temperature. An error of 0.15 gallons would not be important at high delivery rates but is too high to tolerate at rates of about 2 gallons or less. Therefore, temperature should be controlled or at least carefully recorded so compensation can be made in the timer setting to give the desired deposit.

[3]Data are from Table I test numbers 19 through 26.

TABLE I

Variability in deposits of kerosene-dye solutions produced by the spray chamber

| Test[1] No. | Air pressure | Shutter opening | Delivery | Standard deviation | | Standard error | | 95% Confidence limits for average gallons/acre | | Temperature |
|---|---|---|---|---|---|---|---|---|---|---|
| | Lbs./sq. in. | Seconds | Gals./ acre | ±Gals./ acre | ±Per cent | ±Gals./ acre | ±Per cent | ±Gals./ acre | ±Per cent | Degrees F. |
| 1 | 5 | 1 | 9.57 | 0.41 | 4.3 | 0.18 | 1.9 | 0.50 | 5.2 | — |
| 2 | 5 | 1 | 8.65 | 0.14 | 1.6 | 0.06 | 0.7 | 0.17 | 2.0 | — |
| 3 | 5 | 1 | 8.88 | 0.18 | 2.0 | 0.08 | 0.9 | 0.22 | 2.5 | — |
| 4 | 5 | 1 | 8.15 | 0.14 | 1.7 | 0.06 | 0.7 | 0.17 | 2.1 | — |
| 5 | 5 | 1 | 7.36 | 0.41 | 5.6 | 0.18 | 2.4 | 0.50 | 6.8 | — |
| 6 | 5 | 1 | 7.50 | 0.23 | 3.1 | 0.10 | 1.3 | 0.28 | 3.7 | — |
| 7 | 5 | 1 | 8.24 | 0.09 | 1.1 | 0.04 | 0.5 | 0.11 | 1.3 | — |
| 8 | 5 | 1 | 7.46 | 0.18 | 2.4 | 0.08 | 1.1 | 0.22 | 2.9 | — |
| 9 | 5 | 1 | 8.61 | 0.32 | 3.7 | 0.14 | 1.6 | 0.39 | 4.5 | — |
| 10 | 5 | 1 | 8.84 | 0.32 | 3.6 | 0.14 | 1.6 | 0.39 | 4.4 | — |
| 11 | 5 | 1 | 8.56 | 0.18 | 2.1 | 0.08 | 0.9 | 0.22 | 2.6 | — |
| 12 | 5 | 1 | 8.70 | 0.23 | 2.6 | 0.10 | 1.1 | 0.28 | 3.2 | — |
| 13 | 3 | 1 | 2.02 | 0.23 | 11.0 | 0.10 | 4.9 | 0.28 | 13.9 | — |
| 14 | 4 | 1 | 4.14 | 0.18 | 4.3 | 0.08 | 1.9 | 0.22 | 5.3 | — |
| 15 | 5 | 1 | 8.24 | 0.18 | 2.2 | 0.08 | 1.0 | 0.22 | 2.7 | — |
| 16 | 6 | 1 | 9.30 | 0.64 | 6.9 | 0.29 | 3.1 | 0.80 | 8.6 | — |
| 17 | 7 | 1 | 9.71 | 0.41 | 4.2 | 0.18 | 1.8 | 0.50 | 5.1 | — |
| 18 | 8 | 1 | 9.48 | 0.18 | 1.9 | 0.08 | 0.8 | 0.22 | 2.3 | — |
| 19 | 5 | 1 | 6.90 | 0.28 | 4.1 | 0.12 | 1.7 | 0.33 | 4.8 | 62 |
| 20 | 5 | 1 | 6.26 | 0.46 | 7.3 | 0.20 | 3.2 | 0.55 | 8.8 | 61 |
| 21 | 5 | 1 | 6.95 | 0.14 | 2.0 | 0.06 | 0.9 | 0.17 | 2.4 | 66 |
| 22 | 5 | 1 | 7.36 | 0.28 | 3.8 | 0.12 | 1.6 | 0.33 | 4.5 | 68 |
| 23 | 5 | 1 | 7.59 | 0.23 | 3.0 | 0.10 | 1.3 | 0.28 | 3.7 | 71 |
| 24 | 5 | 1 | 8.01 | 0.14 | 1.7 | 0.06 | 0.7 | 0.17 | 2.1 | 73 |
| 25 | 5 | 1 | 8.38 | 0.23 | 2.7 | 0.10 | 1.2 | 0.28 | 3.3 | 76 |
| 26 | 5 | 1 | 8.84 | 0.32 | 3.6 | 0.14 | 1.6 | 0.39 | 4.4 | 78 |
| 27 | 5 | 1 | 9.25 | 0.69 | 7.5 | 0.31 | 3.3 | 0.86 | 9.3 | — |
| 28 | 5 | 1 | 6.77 | 0.18 | 2.7 | 0.08 | 1.2 | 0.22 | 3.2 | — |
| 29 | 5 | 2 | 14.31 | 0.37 | 2.6 | 0.16 | 1.1 | 0.44 | 3.1 | — |
| 30 | 5 | 4 | 27.80 | 0.55 | 2.0 | 0.24 | 0.9 | 0.67 | 2.4 | — |
| 31 | 5 | 4 | 27.25 | 0.69 | 2.5 | 0.31 | 1.1 | 0.86 | 3.2 | — |

[1]In each test, delivery is analysed on five aluminum plates, each sprayed separately.

The estimated change of 0.15 gallons/acre for each 1-degree variation in temperature is not a constant and will shift as the nozzle, air pressure, or timer setting are altered, as well as with the type of liquid used.

The effect of pressure on delivery is not linear. Delivery rises rapidly with increasing pressure up to six pounds/square inch at which point it levels off (see test numbers 13 through 18 in Table I). Actually, the flow rate of a nozzle is about proportional to the square root of pressure (Busvine, 1957) but the amount of spray delivered at a certain point in the receiving chamber is not proportional to the flow rate because higher pressures propel the spray droplets farther.

### References

Busvine, J. R. 1957. A critical review of the techniques for testing insecticides. 208 pp., illus. London.

Drooz, A. T. 1957. Spray chamber insecticide tests on the larch sawfly (*Pristiphora erichsonii* (Htg.)). *Can. Ent.* 89: 183-187.

Eaton, C. B. and J. P. Secrest. 1951. A laboratory spray chamber for producing deposits of limited drop size. *U.S. Bur. Ent. and Plant Quar.* ET – 293, 6 pp., illus., March.

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## Seasonal History of the Balsam Woolly Aphid in the Pacific Northwest

*By* Russel G. Mitchell, Norman E. Johnson, and Julius A. Rudinsky[1]

The balsam woolly aphid, *Chermes* (*Adelges*) *piceae* Ratz., is widely distributed in Europe and North America. It infests many species of *Abies* (true firs) and may be found attacking its hosts at elevations from near sea level to timberline (5,000 to 6,000 feet). Because of the great range of environments inhabited by the balsam woolly aphid, its biology differs considerably from one region to another. Perhaps the most variable feature in its biology is seasonal history. Karafiat and Franz (1956) reported three generations per year in central Europe, whereas Varty (1956) noted two and sometimes a partial third generation in Scotland. Balch (1952) found only two generations in the Maritime Provinces of Canada, but Amman[2] noted three and sometimes a partial fourth generation in southeastern United States.

The widest intraregional variation in balsam woolly aphid seasonal history appears to occur in the Pacific Northwest. Here the insect's most frequent hosts are Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) and subalpine fir (*A. lasiocarpa* (Hook.) Nutt.) at the higher elevations, and grand fir (*A. grandis* (Dougl.) Lindl.) in the lowland valleys. Environment differs considerably between these elevations and so does the seasonal history of the aphid. Studies by the authors have revealed aphid populations producing two generations in the mountains, four generations in the lowlands, and three generations at intermediate elevations. This article reports the results of those investigations, which were conducted independently but cooperatively by Weyerhaeuser Co., Oregon State University, and the U.S. Forest Service.

### Methods and Procedures

Seasonal history studies in Oregon and Washington were begun by the three cooperating agencies in the spring of 1956 and completed by fall, 1959. During

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[2]Quarterly progress report: Oct. 1–Dec. 31, 1959. (Unpublished report, Div. Forest Insect Res., Southeast. Forest Expt. Sta., U. S. Forest Serv., Asheville, N.C.)

TABLE I
Location, host species, and elevation of seasonal history study areas

| Location of study area | Host species | Approximate elevation (feet) |
|---|---|---|
| **High elevation** | | |
| Willamette Pass, near Oakridge, Oreg. | *Abies lasiocarpa* | 4,000 |
| Black Rock, near Grande Ronde, Oreg. | *A. amabilis* | 2,800 |
| Green River, near Mount St. Helens, Wash. | *A. amabilis* | 2,500-3,500 |
| **Intermediate elevation** | | |
| Wind River Arboretum, near Carson, Wash. | *A. alba* and *A. lasiocarpa* | 1,000 |
| **Low elevation** | | |
| Corvallis, Oreg. | *A. grandis* | 230 |

those four years, aphid populations at five different localities were studied—the investigation period in each locality being at least three years. Elevation of the study areas ranged from 230 to about 4,000 feet above sea level (Table I).

Methods of studying the balsam woolly aphid's seasonal history varied with the three authors. Mitchell used two systems: (1) collecting infested bark samples for subsequent laboratory study, and (2) making biweekly field counts of stem populations on permanent 1-inch-square bark plots. All observations were made with binocular microscopes – the field microscope being mounted on an elevator-type camera tripod. The other two authors used methods whereby each insect on a sample area was followed through its development period: one used a microscope grid system for keeping track of the specimens under study (Johnson and Heikkenen, 1958); the other used a method where the locations of individual aphids were marked with insect pins (Tunnock and Rudinsky, 1959).

## Results

Seasonal histories of the aphid in three elevational zones in the Pacific Northwest are summarized in Fig. 1. Only the sistens form of the balsam woolly aphid is referred to in this article. The progredientes stages found in Europe and southeastern Canada have not been observed in Oregon and Washington.

### *Seasonal History at High Elevations*

Environmental conditions at high elevations permitted only two generations per year during the course of this study. The upper chart in Fig. 1 illustrates the seasonal history of the balsam woolly aphid at the higher elevations.

Seasonal history of the aphid begins when the overwintering form of the first generation (hiemosistens generation) breaks diapause in early spring. This initial activity starts about mid-March and extends to late May. It is characterized by a swelling of the first-instar larva and the appearance of a conspicuous glob of colourless "honeydew" at the anal end of the insect. Shortly after the overwintering form begins to swell, it moults and becomes a second-instar larva. Duration of the second stadium is two to three weeks. The insect then moults to the third stage. Length of the third stadium is another two to three weeks, after which the adult is formed. Egg production starts within two or three days after the insect reaches maturity. Adults appearing from mid-June through July have an oviposition period of two to three weeks; those developing earlier,

when temperatures are low, may take four to six weeks to complete oviposition. A very active crawler stage hatches from these eggs.

The newly hatched crawlers represent the beginning of the second (aestivosistens) generation. A few may appear as early as the first week in May, although they do not ordinarily become abundant until June. The peak crawler population occurs in late June or early July. This usually indicates that the first generation is almost completed. After a short wandering period, the crawlers insert their stylets into the bark and enter summer diapause. The resting period lasts from four to six weeks. During late July and early August the population is composed almost entirely of settled first-instar larvae in diapause.

Second- and third-instar larvae become abundant in late August, and by mid- or late-September the adult population reaches its greatest density. Oviposition begins shortly after the appearance of the first adults and ends in late October. With favourable weather, some eggs continue to hatch until late November. Eggs present after November rarely hatch in the field, but may produce crawlers when brought into the laboratory. The first-instar progeny insert their mouth parts into the host, enter diapause, and overwinter in that stage; occasionally, however, a settled insect may moult and pass the winter as a second-instar larva.

*Seasonal History at Intermediate Elevations*

Warmer spring temperatures at intermediate elevations permit earlier development than conditions at higher elevations. Accordingly, at least three balsam woolly aphid generations are completed by fall. The middle chart in Fig. 1 shows the seasonal development of life stages at this elevation.

Spring activity at intermediate elevations begins in early March when the aphids break diapause. By the first of April, second- and third-instar larvae are abundant. A few adults are also present at this time, but they do not reach peak numbers until early May. Because of the slow transition to warm spring temperatures, there is little break between the first and second generations.

Intermediate stages of the second generation appear in significant numbers about the first of June, and the adult population reaches its greatest density in mid-July. Decline of the adult population in the second generation is very fast and quite uniform; consequently, there is a distinct break between the second and third generations. After a two- or three-week quiescent period in which most of the population is in the first-instar resting stage, there is a rapid burst of development. By early October, adults again become abundant; they continue to be present to some degree until late December, although oviposition and hatching seldom occurs after November. As at higher elevations, the balsam woolly aphid overwinters principally as a first-instar larva.

*Seasonal History at Low Elevations*

Seasonal history of the balsam woolly aphid in the lowlands differs from that at intermediate elevations in that part of the population produces a fourth generation. The lower chart in Fig. 1 graphically presents the four generations as found at Corvallis, Oregon.

The Corvallis aphid population, and all other populations observed in Oregon's Willamette Valley, start development very early in the year. Second- and third-instar stages appear about mid-January. By February 1, adults and eggs are usually present, although egg hatch is delayed until about April 1. As at Wind River, there was an overlapping of the first and second generations but a sharp distinction between the second and third generations.

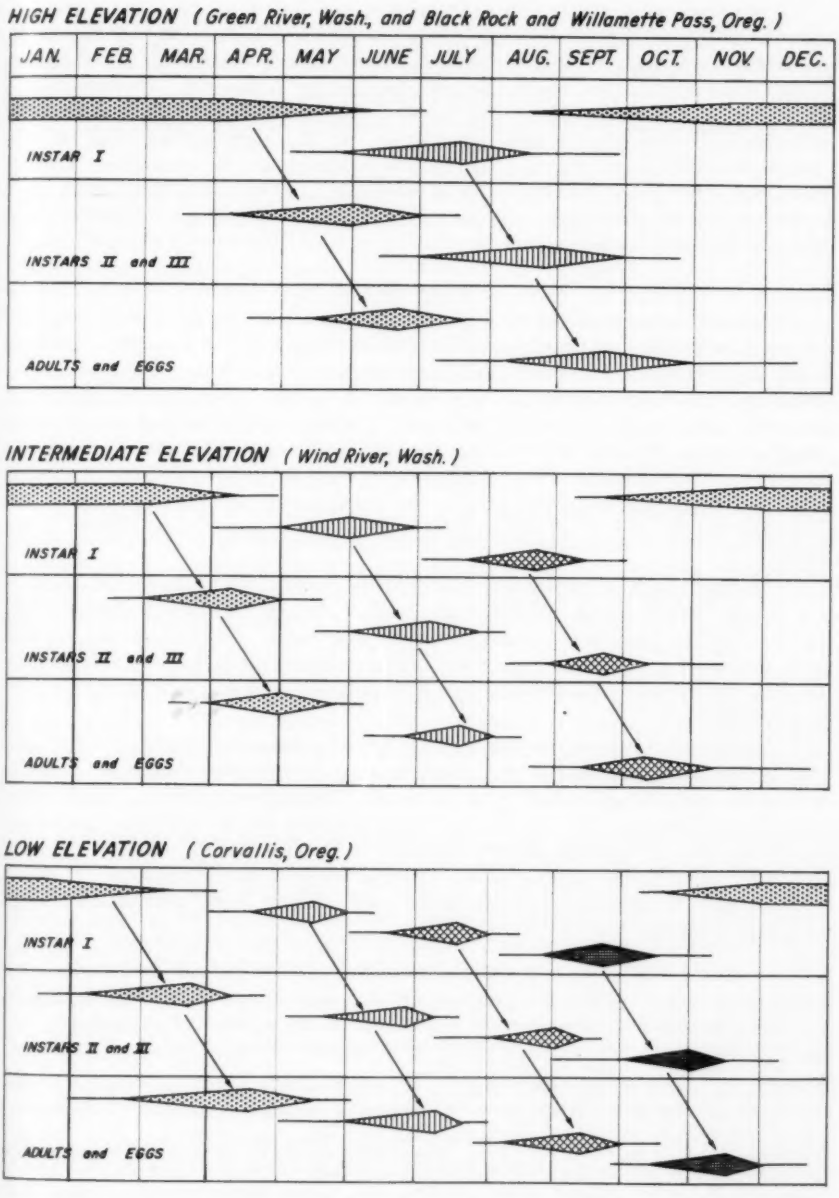
HIGH ELEVATION ( Green River, Wash., and Black Rock and Willamette Pass, Oreg. )
JAN. FEB. MAR. APR. MAY JUNE JULY AUG. SEPT. OCT. NOV. DEC.
INSTAR I
INSTARS II and III
ADULTS and EGGS
INTERMEDIATE ELEVATION ( Wind River, Wash. )
INSTAR I
INSTARS II and III
ADULTS and EGGS
LOW ELEVATION ( Corvallis, Oreg. )
INSTAR I
INSTARS II and III
ADULTS and EGGS
KEY: , 1st generation; , 2nd generation; , 3rd generation; , 4th generation.

Fig. 1. Seasonal occurrence of the balsam woolly aphid (sistens form) at three elevational zones in Oregon and Washington.

Completeness of the fourth generation is variable, depending upon development rate in previous generations. If development is slow, many of the third-generation progeny, especially those hatching in late September or October, settle down and do not resume activity until after January 1. Nevertheless, a significant number of aphids usually break quiescence in September and October and proceed through a fourth generation. In the warmest localities of the Willamette Valley, the fourth generation is probably always complete. One of the authors noted balsam woolly aphid populations in Berkeley, Calif., that were active during the entire year. In that area, there are probably at least four and possibly five generations per year.

## Discussion

Seasonal history of the balsam woolly aphid also varies within localized areas. One factor contributing to this variation is location of host trees. Aphids living on open-grown or stand-edge trees always develop faster than populations infesting trees less exposed. It was found at Green River, for example, that insects on trees located along the edge of a timber stand developed a full month ahead of those 40 feet away within the stand. Similar variation was noted at Corvallis and Willamette Pass. Location of the insects on the trees is another factor affecting seasonal development. In dense stands, aphids situated near the tree base almost always lag one or two weeks behind those living higher on the stem.

Seasonal variation in weather is also an important factor in development of the balsam woolly aphid. Following a mild winter in 1958, insect development started three to four weeks ahead of the previous year. This effect was noticed over the entire region, although it was more pronounced in high-elevation areas. In 1959, the reverse was true when an unseasonably cold and late spring delayed development.

Because of the great variation in the aphid's seasonal history in the Pacific Northwest, data presented in this article cannot be followed explicitly. Checks should be made to see which pattern the local infestations follow. Then, after suitable modification, the information in this article can be applied. The most profitable uses of seasonal-history data have been for timing predator releases, detection surveys, and various phases of balsam woolly aphid research. If direct controls such as application of chemicals are developed, fairly precise knowledge of seasonal history may be needed.

## References

Balch, R. E. 1952. Studies of the balsam woolly aphid, *Adelges piceae* (Ratz.), and its effects on balsam fir, *Abies balsamea* (L.) Mill. *Can. Dept. Agr. Publ.* 867, 76 pp.

Johnson, Norman E., and H. J. Heikkenen. 1958. A method for field studies of the balsam woolly aphid. *J. Econ. Ent.* 51: 540-542.

Karafiat, H., and J. Franz. 1956. Studien zur Populationsdynamik der Tannenstammlaus *Adelges* (*Dreyfusia*) *piceae* Ratz. (Hemiptera, Adelgidae). *Zool. Jb.* (*Systematik*) 84: 467-504.

Tunnock, A., and J. A. Rudinsky. 1959. Observations on the life-cycle of the balsam woolly aphid, *Adelges piceae* (Ratz.), in the Willamette Valley of Oregon. *Can. Ent.* 91: 208-212.

Varty, I. W. 1956. *Adelges* insects of silver firs. *Great Britain, Forestry Comm. Bull.* 26, 75 pp.

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# Effects of Temperatures of Rearing on Reproduction of *Aptesis basizona* (Grav.) (Hymenoptera: Ichneumonidae)

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*Aptesis basizona* (Grav.), a parasite of pine sawflies in Europe, was propagated at Belleville, Ont. (Green, 1938) for release against the European spruce sawfly, *Diprion hercyniae* (Htg.), the European pine sawfly, *Neodiprion sertifer* (Geoff.) and other Diprionidae. Development of the insects in the laboratory was allowed to continue until feeding was completed and cocoons were spun, and was then retarded by placing the insects in cold storage pending shipment to release areas. Frequently stock for propagation was incubated after a period of cold storage, and occasionally the schedule was interrupted by decreases in the reproductive capacity of the adults. It seemed that there was some relationship between the fertility of the adults and the temperatures at which the immature stages were held, both while feeding and after they had reached the fully-fed stage. Experiments were initiated to investigate this hypothesis.

A review of the literature showed that pupae of *Euchalcidia caryobori* Hanna held at 16°C. produced some sterile adult males, the proportion increasing with the length of time, and that females similarly treated produced increasingly fewer eggs (Hanna, 1935). Ijima (1940), working with *Eucosma schistaceana* Sn., found that both males and females that had been held at 32°C. during the pupal stage were sterile. Moursi (1946) found that when pupae of *Nasonia vitripennis* (Wlkr.) were held at temperatures from −1°C. to 16°C. for increasing periods of time there was a gradual decrease in the proportion of females in the progeny. Van Steenburgh (1934) showed that pupae of *Trichogramma minutum* Riley held at 35°F. to 45°F. for 75 days produced adult females that laid one-half the number of eggs laid by those reared at the normal higher temperature.

Techniques were similar to those used in the experiments described by Finlayson (1961). Females were placed individually in Melrose boxes with raisin, moistened dental roll, and one host cocoon of *Neodiprion sertifer* (Geoff.). This cocoon was removed from the box every second day, dissected and examined for eggs, and replaced with a fresh cocoon. The eggs were transferred singly into cocoons of *N. sertifer* and placed immediately in rearing at the temperatures indicated in Table I, or placed at a temperature of 20°C. until fully-fed and cocoons spun, and then placed at the temperatures indicated in that Table. As soon as emergence of adults occurred, at least 20 males and 20 females within each temperature group were mated and the number and sex of the progeny counted. Fecundity of the females was measured by the number of eggs oviposited, and as unfertilized eggs produce male progeny it is assumed that the fertility of the males was indicated by the percentage of females in the progeny.

Rearings at the higher temperatures were in a multiple temperature cabinet, each compartment of which was fitted with both heating and cooling units and controlled by a "Quickset" bimetal thermoregulator (American Instrument Company, 8030-8050 Georgia Avenue, Silver Spring, Maryland, U.S.A.). For work at the lower temperatures, small cabinets each with heating elements, a fan for air circulation, and a "Quickset" thermoregulator, were placed in cold rooms. Temperature readings were taken four times daily and the thermostats adjusted

TABLE I
Average oviposition of adults of *Aptesis basizona* (Grav.) reared in immature stages at the temperatures indicated, and percentages of females in the progeny

| Temperature Degrees C. | From egg stage | | From fully-fed stage | |
|---|---|---|---|---|
| | No. eggs per ♀ | Percentage ♀'s | No. eggs per ♀ | Percentage ♀'s |
| 6 | 11 | 16.0 | | |
| 7.5 | | | 26 | 5.2 |
| 8 | 32 | 18.8 | | |
| 10 | 49 | 21.6 | | |
| 12 | 38 | 18.6 | 36 | 17.9 |
| 14 | 28 | 20.5 | | |
| 16 | 41 | 31.6 | | |
| 18 | 42 | 25.0 | | |
| 20 | 63 | 30.1 | 63 | 30.1 |
| 22 | 68 | 28.5 | 60 | 23.0 |
| 24 | 56 | 30.4 | 65 | 33.9 |
| 24.5 | 50 | 24.8 | | |
| 25.0 | 32 | 15.4 | 15 | 6.1 |
| 25.5 | 32 | 1.9 | | |
| 26.0 | 17 | 1.5 | 35 | 2.7 |
| 26.5 | 6 | 0 | | |
| 28.0 | | | 2 | 0 |

to keep the temperatures constant. Maximum and minimum thermometers were placed in each rearing compartment to reveal if any aberrations in temperature occurred between readings. For the results reported here, the temperatures were mostly constant within ±0.3°C., except in a few cases when the variation was slightly greater.

Of those placed at the temperatures indicated in Table I in the egg stage, adults emerged at all temperatures from 6°C. to 26.5°C., but from 27°C. to 30°C. development did not proceed beyond the third larval instar. Maximum fecundity of the females occurred between 20°C. and 24°C. and decreased to 11 eggs per female at 6°C. and 6 at 26.5°C. Maximum fertility of the males occurred between 16°C. and 24°C., decreased to 16 per cent at 6°C., and to sterility at 26.5°C.

Of those reared to cocoon stage at 20°C. and then placed at the temperatures indicated in Table I, emergence of adults occurred from 7.5°C., the lowest temperature tested, to 29°C. when there was 66 per cent mortality and those adults that emerged did not produce progeny, perhaps because of weakness. No emergence occurred from those reared at 30°C. At the temperatures tested, maximum fecundity of the females and maximum fertility of the males occurred between 20°C. and 24°C., and decreased to 26 eggs per female and 5.2 per cent fertility at 7.5°C. and 2 eggs per female and sterility at 28°C.

It is evident, therefore, that fecundity and sex-ratio of *A. basizona* adults are affected by the temperatures at which the larval stages are held, and that the optimal range is between 20°C. and 24°C.

**Acknowledgment**

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### References

Finlayson, Thelma. 1961. Note on effects of some minerals on fecundity of *Aptesis basizona* (Grav.) (Hymenoptera: Ichneumonidae). *Canadian Ent.* 93: 626-628.

Green (Finlayson), Thelma U. 1938. A laboratory method for the propagation of *Microcryptus basizonius* Grav. *69th Ann. Rept. Ent. Soc. Ontario,* 1938, pp. 32-34.

Hanna, A. D. 1935. Fertility and toleration of low temperature in *Euchalcidia caryobori,* Hanna (Hymenoptera, Chalcidinae). *Bull. Ent. Res.* 26: 315-322.

Ijima, K. 1940. Effect of high temperatures upon the ability of reproduction of *Eucosma schistaceana* Snellen. On the mechanism of sterility caused by high temperatures. (In Japanese) *Oyo Dobuts. Zasshi* 12, No. 5-6, pp. 161-186. (Summary, *Rev. App. Ent.* A, 30: 18).

Moursi, A. A. 1946. The effect of temperature on the sex ratio of parasitic Hymenoptera. *Bull. Soc. Fouad Ier Entom.* 30: 21-37.

Moursi, A. A. 1946. The effect of temperature of development and reproduction of *Mormoniella vitripennis* (Walker). *Bull. Soc. Fouad Ier Entom.* 30: 39-61.

Van Steenburgh, W. E. 1934. *Trichogramma minutum* Riley as a parasite of the oriental fruit moth (*Laspeyresia molesta* Busck.) in Ontario. *Canadian Jour. Res.* 10: 287-314.


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## Effect of the Pea Aphid, *Acyrthosiphon pisum* (Harr.) (Homoptera: Aphididae), on Yields of Alfalfa Hay on Irrigated Land[1]

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Although there are many reports on the control of the pea aphid and its effect on the yield of peas, few are available on the effect of the aphid on the yield of alfalfa hay, particularly on irrigated land. The experiments of Cook and App (1956) and Franklin (1953) were done under climatic and edaphic conditions different from those encountered in southern Alberta. Outbreaks of the aphid occur only occasionally in Alberta, but in 1957 it was very abundant in some irrigated alfalfa fields. This is a report on the effect of the aphid on yields of alfalfa hay in an irrigated area in southern Alberta.

### Materials and Methods

A fairly evenly infested 20-acre hayfield of Grimm alfalfa and brome grass was selected for study. The alfalfa was so heavily infested with aphids that the growing tips were barely visible and the plants were greyish and wilted.

On May 23 the field was sprayed with malathion except for a strip 30 feet wide down the centre. The insecticide was applied at one pint of 50 per cent emulsible concentrate in six gallons of water per acre, with a low-pressure weed sprayer with a 30-foot boom.

Densities of the pea aphid and associated insects were estimated by taking nine samples of 10 sweeps each at intervals of 60 paces in the untreated strip and in one of the contiguous treated strips. The pairs of samples were taken in parallel lines 10 paces apart, immediately before and 1, 4, 11, and 18 days after application of the insecticide. Hay yields were obtained on June 24 by taking nine samples each from the untreated strip and from the treated strip that had been sampled for aphids; areas two yards square were selected at intervals of 60 paces. Yield data were analysed by Student's pairing method.

Pea fields in the area were observed for aphid infestations from May 27 throughout the summer.

[1]Contribution from the Entomology Section.

**Results and Discussion**

The mean number of aphids per sweep were:—

| | Days after spraying | | | | |
|---|---|---|---|---|---|
| | 0 | 1 | 4 | 11 | 18 |
| Untreated | 1,430 | 991 | 945 | 315 | 0 |
| Treated | 1,793 | 643 | 211 | 26 | 1 |

The sharp drop in numbers on both treated and untreated plots on the first day after treatment suggests that some of the spray may have drifted onto the unsprayed strip. Although the effect of the malathion was less rapid than that of several insecticides tested by Franklin (1953), by the fourth day it gave at least the 80 per cent reduction that Cook and App (1956) reported for malathion.

The numbers of the aphid even on the unsprayed strip declined rapidly after the fourth day, and by the 18th day very few remained. Franklin (1953) reported a similar decline on his untreated plots. Evans and Gyrisco (1956) suggested that, as the alfalfa plant slowed in growth and matured, winged migrants developed and flew to annual legumes. Cook and App (1956) stated that when the alfalfa approached blossoming time the winged forms that were produced left the alfalfa for other crops such as peas. In our samples the percentage of winged aphids on each sampling date was:—

| May 23 | May 24 | May 27 | June 3 | June 10 |
|---|---|---|---|---|
| 1.5 | 0.9 | 8.2 | 15.7 | 26.3 |

Thus, the decline in the aphid population was probably due to the increasing production and migration of winged migrants.

The test field was irrigated four days after it had been sprayed, and the alfalfa shortly thereafter lost its wilted appearance and regained its normal colour. None of the plants appeared to be stunted in spite of the high original infestation. Moreover, there seemed to be no difference between the treated and untreated strips even though about 300 to 700 more aphids per sweep were present on the untreated strip than on the treated strip for at least 11 days.

The mean yields of hay in the test, in air-dried weights (tons) 32 days after the insecticide was applied, were:—

| | Alfalfa | Alfalfa and brome |
|---|---|---|
| Untreated | 1.9 | 3.4 |
| Treated | 1.6 | 3.0 |

The differences in yields between treated and untreated plots were not statistically significant. Furthermore, the highest yield of hay from the first cut of an alfalfa-brome mixture in eight years of tests of legume-grass mixtures for hay conducted

at the Lethbridge station by Mr. R. W. Peake and his associates was 1.34 tons per acre. The fact that the yields were as good as those generally obtained in the region when the aphid was not a factor is additional evidence that the high densities of aphids had no effect on the quantity of hay produced. Several other fields of alfalfa in the area had as many aphids as the test field, but because the infestations were patchy they were not treated with insecticide. Later observations showed no apparent differences in plant development between the plants in the infested patches and those from other areas of the same fields.

Cook and App (1956) reported that 100 aphids per sweep were enough to cause stunting and yellowing of alfalfa and that chemical control should be carried out when the aphids exceeded this number. Franklin (1953) reported that 200 to 400 aphids per sweep for about 10 days and only 13 to 75 per sweep for the next seven days were sufficient to reduce the yield by 1.9 tons. Thus, considerable difference in yield might have been expected between our treated and untreated strips. However, the results obtained by Franklin (1953) were from a stand of pure Buffalo alfalfa grown on dry land under droughty conditions. Grimm alfalfa may be more tolerant of the aphid than Buffalo but it appears more likely that irrigation was the most important factor in enabling the plants to recover completely from the aphid attack.

In 1957 the infestations of the aphid in alfalfa fields in southern Alberta occurred early in the growing season. Heavy infestations were observed on May 15. There was still time available after irrigation for the alfalfa to recover before the first cutting of hay was normally taken. As recovery of the alfalfa did not result in a resurgence or prolongation of the infestation the application of insecticide against the aphid was not necessary. Unless infestations develop so late in the season that there is not sufficient time for recovery before haying, or the variety of alfalfa is particularly susceptible to aphid damage, or the aphids are vectors of a disease that affects alfalfa, application of adequate water evidently overcomes the effects of the aphid on alfalfa in southern Alberta.

The application of malathion reduced the numbers of syrphid and coccinellid predators, especially the coccinellids. However, this reduction probably did not influence the results appreciably. Mean numbers of predators per sweep in the test were:—

| | Days after spraying | | | | |
|---|---|---|---|---|---|
| | 0 | 1 | 4 | 11 | 18 |
| Syrphidae, untreated | 0.5 | 0.8 | 0.8 | 1.1 | 0.0 |
| treated | 0.8 | 0.2 | 0.4 | 0.1 | 0.0 |
| Coccinellidae, untreated | 0.3 | 0.3 | 0.8 | 1.6 | 0.1 |
| treated | 0.3 | 0.0 | 0.0 | 0.1 | 0.0 |

Although the numbers of syrphids were reduced on the treated strips, the ratio of syrphids to aphids was not reduced. The principal species of Syrphidae present, as judged from the few adults taken in the sweeps, were *Eupeodes volucris* O.S. (four females), *Scaeva pyrastri* (L.) (three females), and *Sphaerophoria* sp. (one female), and the principal species of Coccinellidae, as judged from the adults taken, were *Hippodamia parenthesis* (Say) (15 specimens), *H. tredecim-punctata tibialis* (Say) (five specimens), and *H. expurgata* Csy. (two specimens).

It might be supposed that the malathion adversely affected the alfalfa in the test, thus masking the effect of its control of the aphids. However, none of the literature on malathion supports this possibility.

**Summary**

In May, 1957, 1,400 to 1,800 pea aphids per sweep were present on an alfalfa field in southern Alberta. Although 80 per cent fewer aphids were present in treated strips than in an untreated strip four days after application of malathion, the reduction in numbers did not result in an increase in the yield of hay. The apparent complete recovery of the infested alfalfa was attributed to irrigation of the field and to the natural decline in aphid numbers resulting from the production of winged migrants. Evidently the pea aphid on alfalfa does not need to be controlled with chemicals in southern Alberta if adequate water is provided for the plants.

**Acknowledgments**

The species of Coleoptera and Diptera were determined by Mr. R. de Ruette and Dr. J. R. Vockeroth, respectively, of the Entomology Research Institute, Canada Department of Agriculture, Ottawa.

**References**

Cook, W. C., and B. A. App. 1956. The pea aphid on alfalfa and peas and its control. *Agr. Chem.* 11(8): 32-35.

Evans, W. G., and G. G. Gyrisco. 1956. Notes on the biology of the pea aphid. *J. Econ. Ent.* 49: 878-879.

Franklin, W. W. 1953. Insecticidal control plot tests for pea aphids in relation to alfalfa hay yields. *J. Econ. Ent.* 46: 462-467.

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## *Mesoleius tenthredinis* Morl. in Pennsylvania and Michigan

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The remarkable discovery that the larch sawfly, *Pristiphora erichsonii* (Htg.), had developed an immunity, in parts of North America, to one of its principal parasites, the ichneumon, *Mesoleius tenthredinis* Morl., followed Lejeune's report (6) that parasitism rarely had exceeded 5 per cent in Manitoba and Saskatchewan since 1940. Muldrew (8, 9) showed that the immunity phenomenon resulted from the formation of a phagocytic capsule around the parasite's egg. The occurrence of parasite resistance by the larch sawfly in Minnesota and Wisconsin was observed in 1952 (2, 4).

The increasing importance of *Larix* spp. for reforestation in New York and Pennsylvania, in particular, is ample stimulus to investigate the status of larch sawfly parasites in these states. Accordingly, prepupae from an outbreak on Japanese larch, *Larix leptolepis* (Sieb. and Zucc.) Gord., in Chenango County, New York, were examined. Here, parasitism by *M. tenthredinis* reached 56 per cent in 1956 before the infestation subsided from this and other mortality factors. The immunity reaction was not evident in the 95 cocoons sampled (3). Other species of parasites were absent.

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TABLE I
Annual parasitism by *Mesoleius tenthredinis* at Renovo, Pennsylvania; results from dissections and rearing

| Cocoons formed | Cocoons dissected | Attacked by *Mesoleius* | Effective attack | Cocoons reared | *Mesoleius* emerged |
|---|---|---|---|---|---|
| Year | Number | Per cent | Per cent | Number | Per cent |
| 1957 | 100 | 7 | 7 | 171 | 10 |
| 1958 | 100 | 14 | 14 | 197 | 13 |
| 1959 | 100 | 48 | 48 | 377* | 45 |
| 1960 | 100 | 12 | 12 | — | — |

*Personal communication from J. A. Muldrew, Forest Biology Laboratory, Winnipeg, Manitoba, October 19, 1960.

*Pennsylvania*

The opportunity to study the parasite situation arose in 1957 in an infestation on Japanese larch between Lock Haven and Renovo, Pennsylvania. Radial increment cores taken from six trees indicated that the outbreak had been severe since 1952. Despite complete or nearly complete defoliation annually from that time to the present, there has been no mortality in the 30-year-old planting.

The Pennsylvania cocoons yielded only one species of larch sawfly parasite, *M. tenthredinis* (Table I); however, some prepupae were killed by the fungus, *Beauveria tenella* (Delac.) Siem., and a few others contained a nematode, *Diplogaster* sp.[2].

In previous outbreaks where the larch sawfly had not developed immunity to *M. tenthredinis*, this parasite appeared to be a major factor in reducing populations. A number of such instances may be cited where, after several generations, *Mesoleius* apparently aided materially in bringing outbreaks to a close: at Thirlmere, England, parasitism amounted to 6, 11, and 62 per cent, respectively, during 1908, 1909, and 1910 (5). Criddle (1) reported 19, 22, 40, and 66 per cent parasitism, respectively, for 1916-1917, 1919-1920, following original releases near Treesbank, Manitoba, in 1913. In British Columbia parasitism was 68, 62, and 55 per cent, respectively, in 1948, 1949, and 1950, and 90 per cent in diapausing sawflies (7). Therefore, it was believed the trend of parasitism in Pennsylvania would rise again in 1960 and be a key factor in the decline of the outbreak. This was not the case, unfortunately. However, annual rearing carried out by Reeks (10) with New Brunswick sawflies, indicated *Mesoleius* parasitized 5, 15, 18, 50, 19, 25, and 45 per cent of the sawflies between 1936 and 1942. These data showed that a sudden drop in parasitism occurred in 1940, but recovery was rapid. It is hoped that the similar decline in parasitism of the 1960 cocoons from Renovo, Pennsylvania, will be of short duration. In any case, proper evaluation of the problem would likely require a minimum of two more seasons' study. It is doubtful that the apparent drop in parasitism in 1960, at Renovo, resulted from a stable parasite population and a fourfold increase of the host population. For, on the basis of severity of defoliation, the sawfly population has been at the saturation level between 1957 and 1960.

It should be possible, therefore, to augment the scant information on larch sawfly outbreaks and the effects of parasitism in plantations by following the Renovo, Pennsylvania, situation until it terminates. This is an area of little

[2]Personal communication from E. A. Steinhaus; Department of Insect Pathology; University of California; Berkeley; August 4, 1960.

TABLE II
Parasitism by *Mesoleius tenthredinis* at various locations in Upper and Lower Michigan (U.P. and L.P. respectively)

| Cocoon formed | County | Cocoons dissected | Attacked by *Mesoleius* | Effective attack | Cocoons reared | *Mesoleius* emergence |
|---|---|---|---|---|---|---|
| Year | | Number | Per cent | Per cent | Number | Per cent |
| 1957 | Iron (UP) | 100 | 14 | 0 | 40 | 0 |
| 1958 | Delta (UP) | 100 | 4 | 2 | 64 | 3 |
| 1959 | Mackinac (UP) | 100 | 12 | 0 | 91 | 2 |
| 1960 | Kalkaska (LP) | 100 | 28 | 4 | — | — |

knowledge at present, but the increasing importance attached to larches for reforestation in the Northeast implies that attention should be given to this problem.

*Michigan*

Upper Michigan is contiguous with Wisconsin and the current sawfly outbreak is part of the great epizootic that reaches across central Canada and the Lake States. Any study of the distribution of the sawfly's immunity to parasitism by *M. tenthredinis* necessarily should include the Upper Michigan population. Therefore, material was examined from Iron County in 1957, and Delta and Mackinac Counties in 1958.

Cocoons from Kalkaska County in Lower Michigan were examined in 1960. The Kalkaska collection is of special interest because Lower Michigan is isolated by Lake Michigan and Lake Huron from the vast outbreak to the north and the west. The findings from these dissections raise a ponderous question regarding the origins of the Kalkaska population.

From the results of these dissections and some rearings, it was apparent that the immunity reaction severely reduced the success of *M. tenthredinis* in Upper and Lower Michigan (Table II). The degree of the immunity in Michigan populations indicates, at least superficially, that these infestations originated from sawfly stocks that dispersed from the general outbreak in central Canada, Minnesota, and Wisconsin. Two additional species of parasites also were found in the Michigan collection: a tachinid, *Bessa selecta* (Meig.), was recovered from dissected material, and the ichneumon, *Aptesis* sp. near *basizona* (Grav.), was reared from the sawfly. The entomophagous fungi, *Isaria farinosa* (Dicks.) Fr. and *Beauveria bassiana* (Bals.) Vuill. were cultured from several of the Kalkaska County specimens, and nematodes, *Diplogaster* spp., were found in two prepupae[a].

In summary, *Mesoleius tenthredinis* populations in Pennsylvania do not appear to be impaired by host, *Pristiphora erichsonii*, immunity. Here, this parasite maintains the potential for playing an important role in terminating larch sawfly outbreaks. In Upper and Lower Michigan, however, the host immunity phenomenon is so strong as to discount this parasite almost completely.

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[a]Personal communications from G. A. Marsh, Department of Insect Pathology; University of California, Berkeley; September 27, 1960, and March 28, 1961.

Nelson of the Pennsylvania Department of Forests and Waters, Harrisburg, for providing cocoons; and the Department of Insect Pathology, University of California, Berkeley, for the determination of infective organisms of the larch sawfly. Also, thanks are due Mr. J. A. Muldrew of the Forest Biology Laboratory at Winnipeg, Manitoba, who kindly provided rearing data for the 1959 Renovo, Pennsylvania, cocoons.

### References

Criddle, Norman. 1928. The introduction and establishment of the larch sawfly parasite, *Mesoleius tenthredinis* Morley, into southern Manitoba. (Hymen.) Canad. Ent. 60: 51-53.

Drooz, A. T. 1953. Larch sawfly investigations in Minnesota, 1952. Jour. Econ. Ent. 46: 826-828.

Drooz, A. T. 1957. The importance of *Mesoleius tenthredinis* Mor., a parasite of the larch sawfly in New York State. Jour. Econ. Ent. 50: 212.

Drooz, A. T. 1960. The larch sawfly, its biology and control. U. S. Dept. Agr., Forest Serv. Tech. Bul. 1212, 52 pp, illus.

Hickson, Sydney J. 1913. The larch sawfly pest in the Lake District. Gard. Chron. January 25, 1913, pp. 49-50.

Lejeune, R. R. 1945. The European larch sawfly. Canad. Dept. Agr., Sci. Serv. Div. Ent., Forest Insect Invest. Bimonthly Prog. Rpt. 1(5): 3.

McLeod, J. H. 1952. Notes on the population and parasitism of the larch sawfly, *Pristiphora erichsonii* (Htg.) (Hymenoptera: Tenthredinidae), in British Columbia. Brit. Columbia Ent. Soc. Proc. (1951) 48: 81-85, illus.

Muldrew, J. A. 1950. *Mesoleius aulicus*, a parasite of the larch sawfly. Canad. Dept. Agr., Sci. Serv., Div. Ent., Forest Insect Invest. Bimonthly Prog. Rpt. 6(6): 2.

Muldrew, J. A. 1953. The natural immunity of the larch sawfly (*Pristiphora erichsonii* (Htg.)) to the introduced parasite *Mesoleius tenthredinis* Morley, in Manitoba and Saskatchewan. Canad. Jour. Zool. 31: 313-332, illus.

Reeks, W. A. 1954. An outbreak of the larch sawfly (*Pristiphora erichsonii* (Htg.)) in the Maritime Province (Hymenoptera: Tenthredinidae) and the role of parasites in its control. Canad. Ent. 86: 471-480, illus.

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## New Species and a New Genus of Melolonthinae From the Southeastern United States (Coleoptera: Scarabaeidae)

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The genus described below appears most closely related to the genus *Gronocarus* Schaeffer (1927, p. 213). The description is based on a unique female collected in eastern Texas within a few miles of the Louisiana state line.

### *Fossocarus*, new genus

Figs. 7, 8, 9

Shining brown. Head behind clypeus, pronotum and basal portion of elytra sparsely pilose. Clypeus semicircular, free margin moderately reflexed, disc flat, posteriorly elevated above frons, sharply delimited by declivous sutural area. Frons and vertex convex, heavily punctate. Eyes scarcely delimited above (a female character in *Gronocarus*), finely faceted, moderately large. Antenna nine-segmented, first segment large and elongate, second segment globular, third and fourth subequal and half the diameter of second, fifth slightly wider than fourth and about as long as wide, sixth much wider than long; seventh, eighth and ninth forming a short, compact club, tips of all three segments sharply

pointed (much more so than in females of either *Gronocarus* or *Hypotrichia*). Labrum rather small, conical, nearly as long as wide, generally similar in size to labrum of females of *Gronocarus*. Mandibles as in *Gronocarus*, but proportionately larger, triangular, rounded at apices. Maxillary palpi four-segmented, first segment minute; second segment slender, approximately as long as terminal segment; third segment slightly wider apically than second, approximately half as long as second; apical segment half again as wide as preceding segment, oval, apex conical. Labium flat, apex round, very similar in shape to labium of *Gronocarus*. Labial palpi three-segmented, short; first segment globular, second segment slightly longer than wide, third segment 1½ times as long as second and with apex conical.

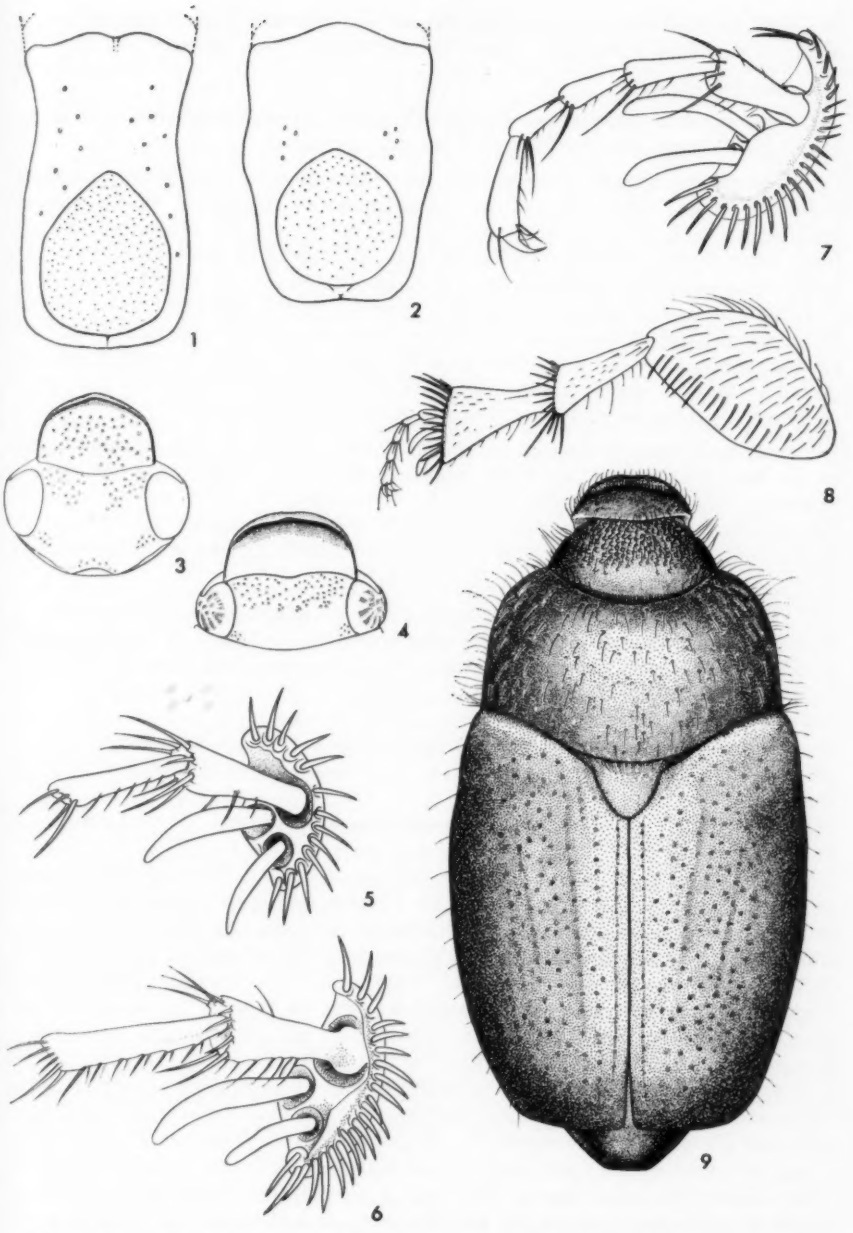
Pronotum strongly convex, sides slightly converging in basal two-thirds (when viewed from above); poorly margined anteriorly and laterally, basal margin obsolete, indicated only by row of fine punctures. Scutellar width slightly greater than one-third elytral width, scutellum with sides and apex rounded. Elytra lacking distinct striae, irregularly punctate, setate basally; apices rounded to almost truncate. Wings lacking, this probably true only of females (as in *Gronocarus*). All coxae very narrowly separated or contiguous. Metasternum medially slightly concave, midline distinctly darker, very slightly elevated. Abdominal segments three to five distinctly connate, transverse sutural lines lacking medially. Legs relatively short and stocky; anterior tibia with two distinct teeth, a third barely indicated slightly behind the middle. Meso- and meta-thoracic tibiae with an outer oblique transverse carina. Metathoracic femur large, proportions of hind legs as in Fig. 8. Apex of hind tibia with two similar, seemingly movable spurs and 25 fairly even spines. All tarsi fairly short, claws not toothed, their bases slightly enlarged, being similar to but shorter and wider basally than claws of *Gronocarus*.

Type-species: *Fossocarus creoleorum*, new species.

### *Fossocarus creoleorum*, new species

Figs. 7, 8, 9

*Holotype*:—Female, length 11.7 mm., width 5.7 mm. Shining brown, vertex slightly darker. Clypeus semicircular, reflexed, more so anteriorly; disc nearly flat, with widely scattered distinct punctures, most numerous in posterior lateral portions. Clypeal sutural area distinctly elevated above the heavily punctate surface of frons. Frons and vertex convex; heavily, densely, irregularly, confluently punctate except in smooth posterior portion of vertex, each large puncture bearing a long erect tan seta. Ventral portions of clypeus relatively long (but not as much as in *Gronocarus*), punctate, each puncture with a long upturned seta. Mouthparts, eyes and antennae as described for genus. Pronotum strongly convex, widest before the middle, sides behind middle almost parallel (when viewed from above), slightly converging; when viewed from side distinctly narrowed posteriorly with posterior angles sharp, nearly right-angled; anterior pronotal angles very obtuse. Pronotal disc with widely scattered, large punctures (Fig. 9), each with a long erect seta; surface between smooth. Elytra as described for genus, the punctures near the humeral angles with long upright setae; elytral margins with widely separated long setae; punctures on rest of elytra with small to minute setae. Pygidium convex, smooth with a few widely scattered, shallow punctures; distinctly margined, the margin slightly thickened apically. Ventral surfaces and legs as described for genus. Sterna laterally with numerous scattered punctures, each bearing a long seta, generally similar




Figs. 1, 3, 6. *Gronocarus multispinosus*, new species; 1, Dorsal view of parameres of male genitalia; 3, Dorsal view of head; 6, Apex of hind tibia and basal two segments of tarsus.

Figs. 2, 4, 5. *Gronocarus autumnalis* Schaeffer; 2, Dorsal view of parameres of male genitalia; 4, Dorsal view of head; 5, Apex of hind tibia and basal two segments of tarsus.

Figs. 7, 8, 9. *Fossocarus creoleorum*, new species; 7, Hind tarsus and apex of hind tibia; 8, Metathoracic leg; 9, Dorsal view of female holotype.

in length and density to setae of females of *Gronocarus*. Female genitalia consisting of two simple triangular plates, abruptly rounded at apices.

*Male*:—Unknown.

*Type material*:—Holotype: Female, Weirgate, Texas, March 28, 1943, B. A. Maina (in Chicago Natural History Museum collection).

This unusual species, although related to *Gronocarus*, undoubtedly deserves a distinct genus. The simple claws, similarity in mouthparts, legs and general body shape all show a strong resemblance to *Gronocarus* but are quite different from other North American melolonthines. Discovery of male specimens may further strengthen the resemblance if they possess wings, since only the females of *Gronocarus* are flightless. The new genus is readily separated from related forms by the raised, semicircular clypeus, convex, heavily punctate frons and vertex, strongly convex pronotum with the scattered, setate punctures, median oblique transverse carina of hind tibiae, flightless condition (probably true only of females) and segments two to five of abdomen being connate.

It seems extremely unusual for a large North American melolonthine beetle to so long escape notice. Here again it resembles *Gronocarus autumnalis* Schaeffer, which was described in 1927. *Gronocarus* is active only in the late fall and very early spring and is seemingly very restricted in habitat, factors which make it rare in collections even today. Similar factors probably explain why *Fossocarus* has for so long escaped detection.

While comparing *Fossocarus creoleorum* to specimens of *Gronocarus*, I found that the population of *Gronocarus* occurring just west of the Appalachicola River in Florida was quite distinct from the species *G. autumnalis* Schaeffer (1927, p. 213), described from Mobile, Alabama. This is not surprising when one considers the flightless condition of the females of *Gronocarus* plus the preferred sand hill environment, which occupies a relatively narrow belt in western Florida and Alabama, and which is transected in several places by river systems.

### *Gronocarus multispinosus*, new species

Figs. 1, 3, 6

*Holotype*:—Male, length 12.5 mm., width 6.1 mm. Dorsally brown with head and base of clypeus nearly black. Clypeus (Fig. 3) semicircular, almost two-thirds as long as wide, moderately reflexed anteriorly; disc flat with numerous scattered punctures, punctures mostly lateral in position; clypeal suture distinct, lightly impressed and vaguely sinuate. Frons and vertex convex (frons of type with an irregular asymmetrical indented line due to injury. Frons and vertex near eyes with scattered punctures; vertex elsewhere smooth and very finely alutaceous. Pronotum nearly identical to that of *G. autumnalis*, anterior margin slightly more deeply emarginate, posterior angles not as strongly explanate, making pronotum appear slightly more convex. Scutellum and elytra not noticeably different from those of *autumnalis*. Pygidium convex with shallow punctures scattered over surface; punctures much shallower and less numerous than in *autumnalis*. Ventral surface of holotype of *multispinosus* differing from that of males of *autumnalis* only in the following characters: abdominal punctures reduced in size and number, hind femur slightly heavier, spines at the apex of the hind tibia (Fig. 6) nearly twice as numerous, 22 spines being present on the apex of the right tibia of the holotype (12 to 14 being normal for *autumnalis* (Fig. 5)). Genitalia (Fig. 1) symmetrical, parameres fused, proportionately longer and wider near apices than in *autumnalis* (Fig. 2).

*Type Material*:—Holotype: Male, De Funiak Springs, Florida, March 18, 1954, in spider web, H. F. Howden (C.N.C. No. 7508). Paratypes: Two males, same data as type (U.S.N.M., Howden); one male, De Funiak Springs, Florida, February 26, 1960, V. O. Kelley (Woodruff); one male, near Clarksville, Florida, March 20, 1954, dead under light, H. F. Howden (Howden).

*Additional Specimens Referred to this Species*:—Four males, four females, Panama City, Florida, November 16, 1959, December 7, 22, 1959, on St. Augustine grass lawn, C. W. Hollister (Woodruff).

Variation in the small series of type material is slight. Length varies from 12.6 to 13.6 mm. and width from 6.1 to 6.7 mm. All of the paratypes have fewer punctures on the pygidium than does the type, one specimen having the pygidium nearly impunctate. The greatest variation seems to occur in the number of spines on the apex of the hind tibia, which ranges from 15 to 23, the average being 19 or 20. Three of the De Funiak specimens were taken in spider webs and two of the specimens are lacking antennae and some dorsal setae. The Clarksville specimen, which was found dead under a light, is lacking the head. The area where the specimens were found was typical southeastern sand-hill country, the vegetation consisting largely of turkey oaks and wire grass.

The Panama City specimens are not included in the type series, since they show just enough differences to suggest the possibility that they represent a distinct population. Since in this genus all of the females are flightless, the metasternal wings being reduced to little more than buds, the existence of distinct races separated by seemingly minor ecological barriers is not unlikely. The Panama City specimens resemble the type of *multispinosus* in the shape of the clypeus, in the length of the fused parameres of the male genitalia, and in the relatively few punctures on the pygidium. The number of spines of the apical margin of the hind tibia varies from 14 to 19 in the males and from 12 to 14 in the females. In this character the Panama City specimens appear to be intermediate, since 19 to 20 or more spines is normal for the males of typical *multispinosus* and 12 to 14 spines for the males and 10 spines for the females is normal in *autumnalis*. In addition to the difference in the spines on the legs, the Panama City population lacks the distinctive clypeal punctures of *multispinosus* and in most examples the clypeus is more distinctly reflexed. These differences may or may not be significant when more material is collected. Despite the differences in the spines and clypeus, the Panama City specimens certainly appear to be more closely related to the De Funiak-Clarksville populations of *multispinosus* than to *autumnalis*.

*Gronocarus multispinosus* can easily be separated from *G. autumnalis* (Figs. 2, 4, 5), the only other species in the genus, by its larger clypeus with relatively flat, normally punctate disc; the lightly, sparsely punctate pygidium; slightly larger average size; the numerous (15 to 23) spines on the apex of the hind tibia; and the more elongate parameres of the male genitalia.

**Summary**

A new melolonthine genus, *Fossocarus*, is described and a single new species from east Texas, *creoleorum*, is included. Its relationship with *Gronocarus* is discussed, and a new species of *Gronocarus* from Florida, *multispinosus*, is described.

**Acknowledgments**

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Chicago Natural History Museum; Mr. O. L. Cartwright, United States National Museum, Washington, D.C.; and Mr. Robert Woodruff, Entomology Section, Division of Plant Industry, Florida Department of Agriculture, Gainesville, Florida, for the loan of some of the specimens used in this study.

### Reference

Schaeffer, Charles. 1927. On a few new and known melolonthine Scarabaeidae (Col.). *Bull. Brooklyn Ent. Soc.* 22:213-216.

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## Bioassay of Organic Insecticides, in Terms of Contact Toxicity, to the Black Cutworm, *Agrotis ypsilon* (Rott.)[1]

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### Introduction

In recent years the black cutworm, *Agrotis ypsilon* (Rott.), has been the predominant species of economic importance in southwestern Ontario. Relatively small populations of this insect can cause extensive damage to widely-spaced cash crops such as tobacco, tomatoes, and sugar beets.

Present control recommendations are based primarily on results obtained from field trials. These results are often inconclusive because cutworm outbreaks are difficult to predict and usually unevenly distributed. Therefore, it is necessary to develop laboratory techniques to assist in assessing the comparative toxicity of insecticides and their formulations.

Development of the present technique was carried out with two objectives: first, to accumulate toxicity data for insecticides presently in use, as reference standards when testing potential insecticides; secondly, to establish which insecticides should be used in field trials. To encompass both of these objectives it was necessary to develop a standardized bioassay procedure rather than a screening method.

Since cutworms are poisoned by contact with insecticides in various formulations, it is possible to assess insecticide toxicity by direct contact bioassay with solutions of analytical grade insecticides. No doubt such factors as environmental conditions and formulation will affect toxicity. However, separate procedures must be developed to assess the effect of these factors.

Workers in the field of insect toxicology have developed a number of direct contact bioassay procedures. These procedures are reviewed by Busvine (1957) and Shepard (1958). Brown *et al.* (1947) used the spray tower technique developed by Tattersfield and Morris (1924); fifteen organic insecticides were tested against several insects, including the pale western cutworm, *Agrotis orthogonia* Morr. Weinman and Decker (1951) tested eight organic insecticides for both contact and stomach action against the armyworm, *Pseudaletia unipuncta* (Haw.).

### Methods and Materials

The bioassay procedure was adapted from the method of Brown *et al.* (1947). The spray tower (Figure 1) consisted of a glass cylinder, 12 inches in diameter and 26½ inches high, set upon a stainless steel and aluminum base plate

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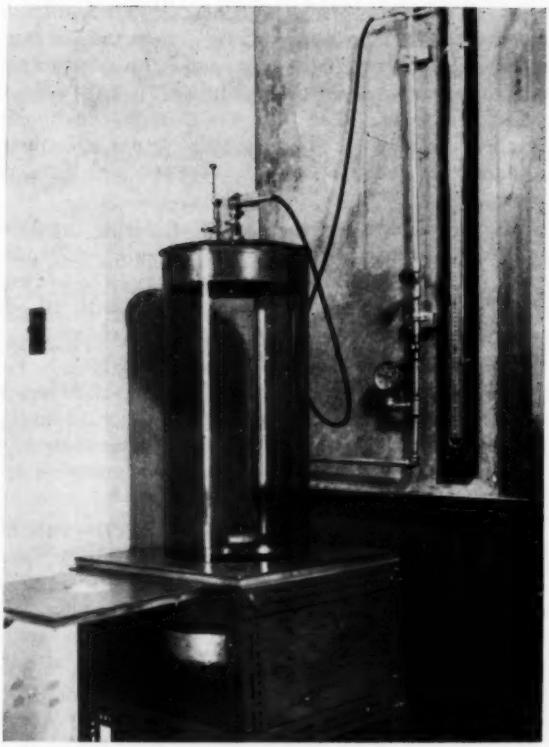

Fig. 1. Spray tower constructed for bioassay of insecticides against the black cutworm.

one inch in thickness. A circular area 11¾ inches in diameter was cut out in the centre of the base plate. A movable stainless steel and aluminum panel was inserted on rollers fastened to the lower surface of the base plate. A circular area one-half inch deep and 3½ inches in diameter was recessed into the panel in such a position that when the panel was pushed into place, the recessed area was directly under, and exactly 28 inches from, the spray nozzle which was fastened in the centre of a galvanized iron lid.

Spray was applied through a De Vilbliss nozzle, No. 631. Air pressure was maintained at 23 cm. Hg. by a reducing valve and manometer. Since a 9:1 acetone-olive oil solvent mixture exhibited no toxicity to the test insects, it was adopted as the "standard" insecticide solvent. Insecticide solutions were made by dilution of a standard molar concentration. Five millilitre aliquots of insecticide solution were used for each application. Spray was applied for 30 seconds and a 30-second settling period was allowed.

The tower was connected to an adjacent fume hood by means of a flexible pipe 2½ inches in diameter. When the sliding panel was withdrawn, fumes contained in the tower were evacuated into the hood. Upon completion of tests with an insecticide, the tower was washed with a stream of acetone. Excess acetone was collected in a galvanized iron pan which could be raised or lowered by a foot lever.

Fourth-instar larvae of the black cutworm, *Agrotis ypsilon* (Rott.), reared according to the method of Harris *et al.* (1958), were used as test insects. Each insecticide was assayed against both the ninth and tenth generations of laboratory-reared larvae. Ten larvae were introduced into a 3½-inch petri dish lined with No. 1 Whatman filter paper. The dish was then placed in the recess of the sliding panel of the spray tower. The larvae were not anaesthetized since both carbon dioxide and ether resulted in slow recovery and high mortality in the controls.

The following insecticides were screened:— aldrin[1] (assay 99.7 per cent), DDT[2] (98 per cent), dieldrin[3] (100 per cent), Dylox[4] (100 per cent), endrin[5] (98.3 per cent), Guthion[6] (95 per cent), heptachlor[7] (99.3 per cent), malathion[8] (99.6 per cent), PVP-Iodine[9] (polyvinyl pyrrolidone with 10 per cent Iodine), Sevin[10] (100 per cent), and toxaphene[11] (67-69 per cent chlorine).

Initial screening tests were conducted using $3 \times 10^{-3}$, $3 \times 10^{-4}$, $3 \times 10^{-5}$, and $3 \times 10^{-6}$ molar solutions. Those compounds showing no toxicity at $3 \times 10^{-3}$ molar were considered of insufficient toxicity to be of value. Insecticide concentrations were calculated on a molar rather than a percentage basis since toxicity is actually dependent on the molecular composition of the sample rather than the gram weight (Lord, 1948).

For the assays proper, four to six insecticide molar concentrations causing mortality within a 20 to 85 per cent range were tested. Duplicate groups, each containing 10 larvae, were used with each insecticide concentration. Tests with dieldrin, which was used as a "standard" insecticide, were included with assays on each "test" insecticide. Two solvent controls were included with each bioassay.

After being sprayed, larvae were placed for observation in waxed paper cups, 2½ inches in diameter and 2¼ inches high, containing a one-inch layer of sifted sandy loam soil with five per cent added moisture (v/v). A one-inch layer of this soil was then placed over the treated larvae. One-half inch cubes of Beck's diet (Beck *et al.*, 1949) were supplied as food. The observation containers were placed in an incubator maintained at 80° ± 1°F. and 75 ± 5 per cent relative humidity.

Mortality counts were made at 24 and 48 hours. In making counts, the photonegative and thermonegative responses of the larvae were used. The larvae were placed on a white circle, four inches in diameter, contained on a black wooden panel 12 inches square. The panel slid into a 12-inch cubic black box. Heat and light were provided by a 40-watt bulb fastened to the top of the box. An aluminum cylinder three inches in diameter and 10 inches long was fitted around the bulb and served to focus light and heat directly on the white area of the panel. As soon as the light was turned on, normal larvae moved toward the darker and cooler areas of the box. Larvae unable to move outside the white circle within one minute were classified as dead.

The 48-hour dosage-mortality data were analysed by probit analysis. Corrections for natural mortality were made using Abbott's formula (Abbott, 1925) and modified weighting coefficients (Finney, 1952).

[1]Shell Chemical Corporation, Denver, Colo.
[2]Geigy Chemical Corporation, Yonkers, N.Y.
[3]Shell Chemical Corporation, Denver, Colo.
[4]Chemagro Corporation, New York, N.Y.
[5]Shell Chemical Corporation, Denver, Colo.
[6]Chemagro Corporation, New York, N.Y.
[7]Velsicol Corporation, Chicago, Ill.
[8]American Cyanamid Company, New York, N.Y.
[9]General Aniline and Film Corporation, New York, N.Y.
[10]Union Carbide Chemicals Company, New York, N.Y.
[11]Hercules Powder Company, Wilmington, Del.

**Results and Discussion**

In screening tests, the only compound showing no toxicity at $3 \times 10^{-3}$ M. was PVP-Iodine. The remaining insecticides were bioassayed. A summary of the results of the statistical analysis of the dosage-mortality data is shown in Table I.

The primary objective of this work was to establish the relative toxicities of insecticides in general use, for comparison with tests of compounds showing potential value in cutworm control. It was necessary, therefore, to devise a method for calculation of these relative toxicities.

Although the position and slope of the regression line for a particular insecticide may vary from one test to another, the relative toxicity of two insecticides may be expected to be more stable. The inclusion of a "standard" insecticide with each test insecticide affords a test of this hypothesis, and the results of these experiments tend to confirm it. With Guthion, for example, LD50 values in two separate assays were 560 and $330 \times 10^{-5}$ M., while the corresponding values for dieldrin were 33 and $25 \times 10^{-5}$ M. Because the values for both insecticides changed in the same direction and in roughly the same proportion, the estimated relative toxicities for the two assays were relatively stable, having values of 0.059 and 0.076. The slopes of the regression lines also changed in a similar fashion so that the relative toxicities at other levels of kill were more stable than the individual lethal dose estimates. The data are illustrated in Figure 2.

It is, therefore, advantageous to present the results in terms of toxicity relative to a "standard" insecticide. If the regression lines within any one assay could be assumed to be parallel, then the relative toxicity could be assumed to be independent of the level of kill. In these experiments, however, the slopes for some of the insecticides, notably Dylox, Guthion, malathion, heptachlor, and Sevin were lower than for dieldrin, so that the relative toxicities changed with the level of kill. This introduces a difficulty in presentation and interpretation of the results: relative toxicities at the 50 per cent mortality level can be estimated with the best precision, but may be misleading so far as relative toxicities at higher levels of kill are concerned. It is advisable, therefore, to consider estimates of relative toxicity at the 95 per cent mortality level as well as at the 50 per cent mortality level. Therefore, the relative toxicities at both the LD50 and LD95 levels in the separate assays were tested for homogeneity as described by Bliss (1952). Since the agreement between the assays was good compared with the within assay error, the separate relative toxicities were combined using weighted means. The combined values are given in Table II with their fiducial limits.

The insecticides have been listed in Table II in order of decreasing toxicity, relative to dieldrin at the 50 per cent mortality level. Dieldrin has a numerical value of one. Hence, at the 50 per cent mortality level, aldrin is 2.469 times as toxic as dieldrin, while toxaphene is 0.011 times as toxic. Although the relative toxicity estimates at the LD50 and LD95 levels varied for some insecticides, the order of toxicity at both levels was much the same. The only striking difference was the reversal in performance of aldrin and heptachlor, aldrin being approximately twice as toxic as heptachlor at the 50 per cent mortality level and 15 times as toxic at the 95 per cent mortality level. At the 50 per cent mortality level, heptachlor was approximately seven times as toxic as DDT, but at the 95 per cent mortality level it was equal in toxicity.

The chlorinated hydrocarbon insecticides were generally more toxic to cutworms than the organic phosphate group, primarily because of the steep slope

TABLE I
Summary of dosage-mortality data obtained from bioassay of organic insecticides against fourth-instar larvae of the black cutworm, *Agrotis ypsilon* (Rott.)

| Compound | Assay No. | Test insecticide | | | Standard insecticide (dieldrin) | | |
|---|---|---|---|---|---|---|---|
| | | Slope | LD50 (x $10^{-5}$ M.) | LD95 (x $10^{-5}$ M.) | Slope | LD50 (x $10^{-5}$ M.) | LD95 (x $10^{-5}$ M.) |
| Endrin | 1 | 2.147 ± 0.772 | 14 | 82 | 3.107 ± 0.878 | 33 | 112 |
| | 2 | 2.778 ± 0.539 | 13 | 51 | 2.755 ± 0.835 | 33 | 131 |
| Aldrin | 1 | 3.708 ± 0.865 | 27 | 76 | 2.133 ± 0.745 | 34 | 200 |
| | 2 | 3.803 ± 1.829 | 29 | 77 | 3.541 ± 0.951 | 42 | 122 |
| Heptachlor | 1 | 1.461 ± 0.721 | 43 | 580 | 2.948 ± 0.787 | 31 | 117 |
| | 2 | 1.166 ± 0.358 | 38 | 974 | 3.337 ± 0.867 | 30 | 93 |
| Dylox | 1 | 1.797 ± 0.657 | 198 | 1626 | 3.107 ± 0.878 | 33 | 112 |
| | 2 | 1.833 ± 0.546 | 203 | 1601 | 3.307 ± 0.130 | 27 | 85 |
| DDT | 1 | 3.623 ± 0.970 | 310 | 523 | 2.754 ± 0.810 | 37 | 147 |
| | 2 | 4.168 ± 1.066 | 310 | 755 | 3.175 ± 0.908 | 25 | 83 |
| Sevin | 1 | 1.037 ± 0.266 | 310 | 11820 | 3.215 ± 0.840 | 45 | 145 |
| | 2 | 1.452 ± 0.479 | 360 | 4820 | 3.686 ± 0.912 | 50 | 143 |
| Guthion | 1 | 1.093 ± 0.406 | 560 | 17940 | 3.107 ± 0.878 | 33 | 111 |
| | 2 | 1.464 ± 0.360 | 330 | 4393 | 3.175 ± 0.908 | 25 | 83 |
| Malathion | 1 | 1.485 ± 0.394 | 1150 | 14730 | 3.279 ± 0.790 | 42 | 85 |
| | 2 | 1.775 ± 0.549 | 1380 | 11630 | 3.240 ± 0.792 | 41 | 131 |
| Toxaphene | 1 | 2.947 ± 0.235 | 3300 | 11770 | 3.279 ± 0.790 | 42 | 85 |
| | 2 | 2.945 ± 0.753 | 2800 | 10140 | 3.318 ± 0.713 | 27 | 83 |

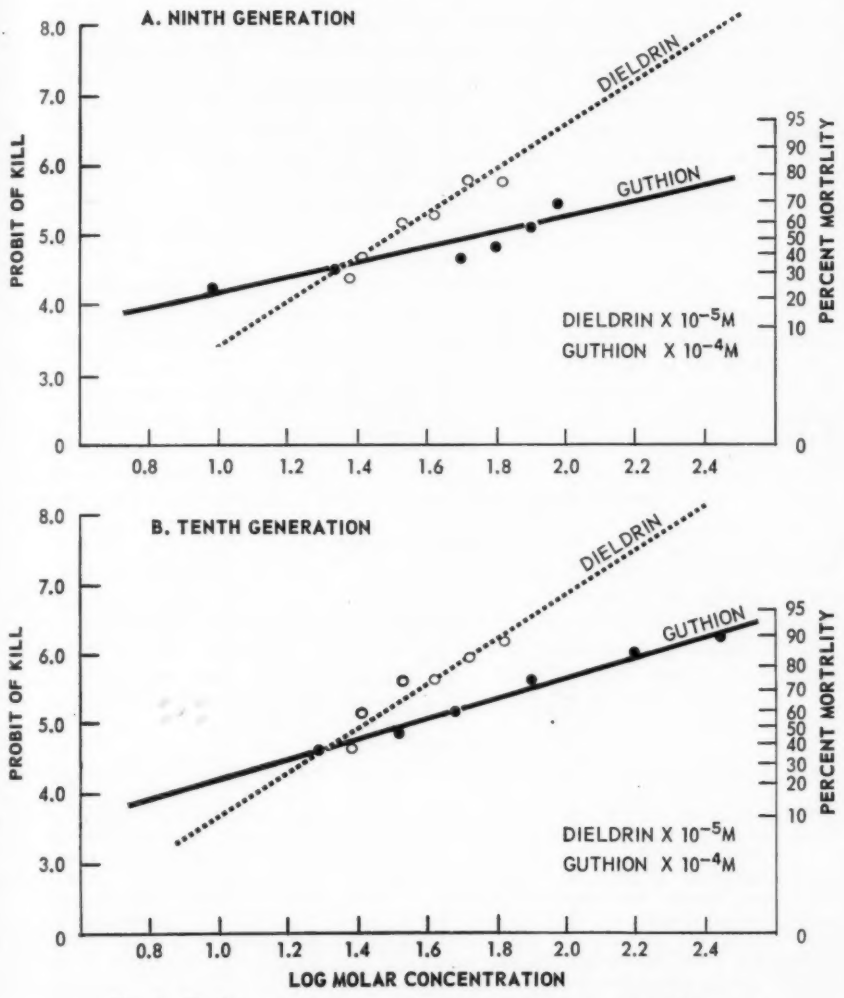


Fig. 2. Toxicity of Guthion to fourth-instar black cutworm larvae.

of the regression line. Endrin, aldrin, and dieldrin were highly toxic. DDT, although less toxic gave a similar steep regression line. The values obtained with heptachlor were difficult to reconcile with the excellent control obtained with this compound in carefully controlled field experiments (Begg *et al.*, in preparation). It seems likely that time, as well as toxicity, is a factor in this case, with heptachlor being slightly slower in action than aldrin and dieldrin but ultimately giving as good control. Sevin, a carbamate, was slightly more toxic than DDT at the 50 per cent mortality level, and considerably less toxic at the 95 per cent mortality level (see Table II).

Although the organic phosphate insecticides appeared to be less toxic than the chlorinated hydrocarbons, we consider that Dylox and Guthion warrant further testing under field conditions.

TABLE II

Toxicities relative to dieldrin (weighted means of two assays)
(dieldrin = 1)

| Compound | 50% mortality | | 95% mortality | |
|---|---|---|---|---|
| | Relative toxicity | Fiducial limits | Relative toxicity | Fiducial limits |
| Endrin | 2.469 | 3.194 & 1.909 | 2.106 | 4.126 & 1.075 |
| Aldrin | 1.372 | 1.681 & 1.120 | 1.956 | 4.397 & 0.871 |
| Heptachlor | 0.740 | 0.972 & 0.533 | 0.129 | 0.976 & 0.017 |
| Dylox | 0.150 | 0.204 & 0.110 | 0.058 | 0.160 & 0.021 |
| Sevin | 0.144 | 0.214 & 0.097 | 0.019 | 0.079 & 0.005 |
| DDT | 0.106 | 0.132 & 0.086 | 0.129 | 0.236 & 0.070 |
| Guthion | 0.066 | 0.095 & 0.046 | 0.016 | 0.046 & 0.005 |
| Malathion | 0.037 | 0.049 & 0.028 | 0.007 | 0.023 & 0.002 |
| Toxaphene | 0.011 | 0.014 & 0.009 | 0.008 | 0.013 & 0.007 |

The present method only takes into consideration the actual amount of toxicant necessary to kill fourth-instar *Agrotis ypsilon* (Rott.) larvae by contact. Further work is necessary to determine the contact toxicity of these insecticides to the remaining larval instars, the toxicity of these compounds when incorporated in soils, and toxicity in relation to time. In the results presented above, approximately eight to nine times as much DDT as dieldrin is required for equal toxicity. However, if the period of time available for obtaining cutworm control could be doubled, the concentration of DDT necessary could no doubt be reduced to a considerable extent.

**Summary**

A laboratory technique for testing the contact toxicity of insecticides to the black cutworm, *Agrotis ypsilon* (Rott.), is described. The toxicities of 10 organic insecticides relative to a standard insecticide, dieldrin, were determined. Primarily because of the steep slope of the regression lines, the chlorinated hydrocarbon insecticides were more toxic than the organic phosphates. Endrin, aldrin, and dieldrin were the most toxic insecticides tested. Of the phosphates tested, Guthion and Dylox were the most toxic being only slightly less toxic than DDT. Sevin, a carbamate, was slightly more toxic than DDT at the 50 per cent mortality level but less toxic than DDT at the 95 per cent mortality level.

**Acknowledgments**

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**References**

Abbott, W. S. 1925. A method of computing the effectiveness of an insecticide. *J. Econ. Ent.* 18: 265-267.

Beck, S. D., J. H. Lilly, and J. F. Stauffer. 1949. Nutrition of the European corn borer, *Pyrausta nubilalis* (Hbn.) I. Development of a satisfactory purified diet for larval growth. *Ann. Ent. Soc. America* 42: 483-496.

Begg, J. A., C. R. Harris, and G. F. Manson. Control of an artificial infestation of the black cutworm, *Agrotis ypsilon* (Rott.), in flue-cured tobacco with five soil insecticides. In preparation.

Bliss, C. I. 1952. Statistics of Bioassay, Section VIII, 1A.

Brown, A. W. A., W. W. Hopewell, B. J. Wenner, and H. McDonald. 1947. Laboratory assessment of organic insecticides for control of certain lepidopterous larvae. *Canad. Ent.* 79: 161-166.

Busvine, J. R. 1957. A critical review of the techniques for testing insecticides. Eastern Press Limited, London, England.

Finney, D. J. 1952. Probit analysis. A statistical treatment of the sigmoid response curve. Cambridge University Press, Cambridge, England.

Harris, C. R., J. A. Begg, and J. H. Mazurek. 1958. A laboratory method of mass rearing the black cutworm, *Agrotis ypsilon* (Rott.), for insecticide tests. *Canad. Ent.* 90: 328-331.

Lord, K. A. 1948. The contact toxicity of a number of DDT analogues and of four isomers of benzene hexachloride to *Macrosiphoniella sanborni* and *Oryzaephilus surinamensis*. *Ann. App. Biol.* 35 (4): 505-526.

Shepard, H. H. 1958. Methods of testing chemicals on insects. Vol. I. Burgess Publishing Company, Minneapolis, Minnesota.

Tattersfield, F., and H. M. Morris. 1924. An apparatus for testing the toxic values of contact insecticides under controlled conditions. *Bull. Ent. Res.* 14: 223-233.

Weinman, C. J., and G. C. Decker. 1951. The toxicity of eight organic insecticides to the armyworm. *J. Econ. Ent.* 44: 547-552.

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# Design of a Sampling Plan for Studies on the Population Dynamics of the Diamondback Moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae)

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In 1958, intensive studies on the population dynamics of the diamondback moth, *Plutella maculipennis* (Curt.), on cabbage were initiated in long-term study plots at Merivale, Ontario. The object was to construct ecological life tables (Morris and Miller, 1954) for successive generations of the insect, and, ultimately, to develop a mathematical model describing survival of field populations. This paper reports on the variation between samples of immature stages of the moth, and between some of the mortality factors affecting its abundance, and on the use of these data in designing a sampling plan with acceptable limits of precision.

The use of life tables in insect epidemiology has lagged behind that for other organisms. In North America, ecological life tables that are reasonably complete have been developed for only a handful of insect species. Morris *et al.* (1958) have developed life tables for the spruce budworm, Stark (1959) for the lodgepole needle miner, and LeRoux and Reimer (1959) for two species of apple pests. All of these studies dealt with insects that attack perennial crops, and that have not more than a single generation per year. The present study concerns an insect that attacks an annual crop, and that has several generations per year.

## Status of the Pest

The diamondback moth is a small plutellid that attacks cabbage and related crops throughout Canada. Although not frequently reported in destructive numbers, it is always present, and may develop from endemic to epidemic levels in a very short period of time. An epidemic may originate during a single generation of the species, or may originate during the course of several generations. Infestations may be local, or widespread as in 1958 (MacNay, 1959). Although not abundant in Ontario generally, the moth has been extremely numerous in the eastern part of the Province since late 1951.

The diamondback moth has four to six generations per year in eastern Ontario (Harcourt, 1957b). It does not hibernate there, and annual infestations arise from adults that overwinter in more southerly regions and migrate north in the spring as the weather moderates. The immigrants arrive in eastern Ontario during late May. If few cultivated crucifers are available for egg-laying, as is frequently the case, many first generation eggs are laid on cruciferous weeds. Later generations develop almost exclusively on cultivated crucifers. All stages of the insect except the moth in flight are found on the plant. The larvae feed on the foliage during all of the four instars, mining the leaves during the first. There is little plant-to-plant dispersal of immature larvae. However, mature larvae often migrate for short distances in search of suitable pupation sites, leaving densely occupied plants in favour of less occupied ones.

Two crops of cabbage are grown commercially in eastern Ontario. The early crop, which matures in July, is planted in late May; the late crop, which matures in October, is planted in late June. Both crops are attacked by the insect. The early crop is preferred by ovipositing adults until about mid-July when the heads reach maturity; the late crop has by then become well established and is of sufficient size to be of stronger attraction.

### Experimental Plots

The experimental plots (Fig. 1; early cabbage, late cabbage) were located at a summer field station, Merivale, Ontario, five miles south of the Central Experimental Farm, Ottawa. Each plot consisted of 5000 plants, and occupied approximately one-half acre. The plots were bordered on the south and east by several acres of forage and pasture land, on the north by open cultivated fields, and on the west by a commercial garden area containing various vegetables, chiefly corn and potatoes. The rows were spaced 36 inches apart with plants at 18-inch centres in the row. The soil was of a light standy loam, pH 6.8. Clean cultivation was practised throughout the study, and at no time were insecticides used on or near the experimental plots.

In accordance with commercial practice, two crops of cabbage were grown each year. The early crop, variety Golden Acre, was set out at mid-May, in sufficient time to attract ovipositing adults of the immigrating generation. The late crop, variety Penn State Ballhead, was planted in late June. The early crop was harvested and disced down at the end of July; the late crop was allowed to stand until the following spring. Life table data were recorded for generations one and two on the early crop, and for generation two (concurrent with the early crop) and succeeding generations on the late. Since the two plots were exactly the same size, the data for generation two may be ultimately combined in a single life table.

### Sampling Methods

*Sample Unit*

The sample unit upon which the life tables are based is the crown quadrant. It was obtained by dividing the foliage, or crown, of the plant into four quadrants, designated N, E, S, and W, according to the four cardinal points of the compass (Fig. 2). This unit, selected after the criteria of Morris (1955), is stable, and contains all the immature stages of the insect. It is reasonably small, and is easily delineated in the field, thus lending itself well to a number of random sampling designs. Use of this unit readily permits estimates of absolute population (population per plant or acre).

*Sampling Procedure*

To compare variation between samples of the immature stages, and of related mortality factors, within the crown of the plant, and between plants, the plots were divided into four blocks of equal size. At each sampling, 16 plants were selected at random from each block, a total of 64 plants. The plants were sectioned in the field and examined leaf by leaf. As the crown of each plant was composed of four quadrants, a total of 256 sample units were examined on each date. Population densities of the immature stages of the moth were estimated by direct sampling; those of parasites were obtained by collecting and rearing the host at certain critical periods in its life history.

In 1958, for reasons that follow, each of the four blocks was marked off by means of a $4 \times 4$ grid into 16 strata of equal size. At each sampling, a single plant was examined per stratum.

*Population Distribution*

Knowledge of the spatial pattern of an insect may be used to advantage in the design of sampling. It was recognized in the early stages of the present study that the frequency distribution of counts of the immature stages of the diamondback moth did not conform to the Poisson series, there being an excess

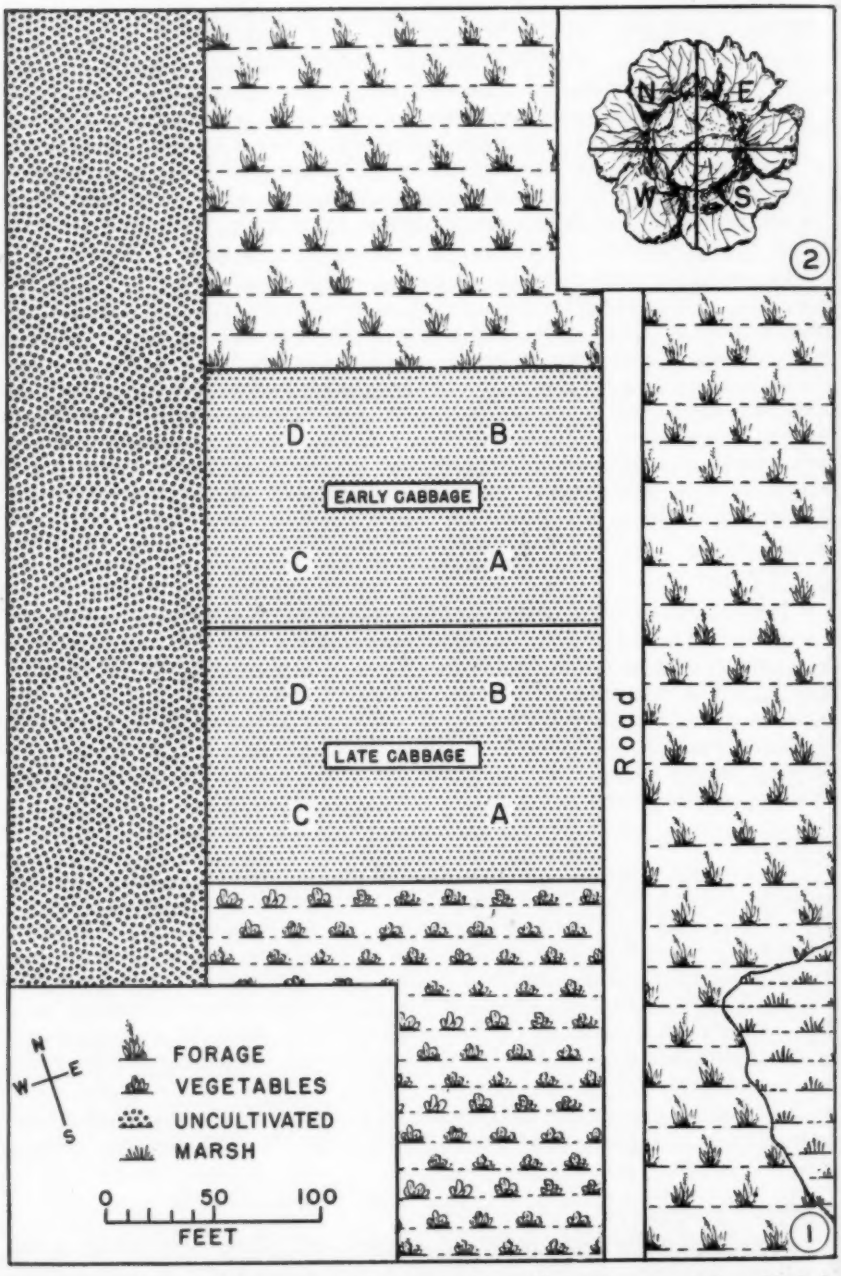


Fig. 1. Diagram of the experimental cabbage plots and immediate surroundings, Merivale, Ontario.

Fig. 2. Drawing of the crown of a cabbage plant, with quadrants indicated.

of uninfested plants and heavily infested plants over the expected number. The observed distributions, however, closely approximated the negative binomial series (Harcourt, 1960b). Calculations of the exponent *k* indicated that the distribution increased in randomness with development of the insect. It was thus anticipated that the required degree of sampling precision could be obtained with fewer samples of pupae, than say, eggs.

In experimental plots containing an annual crop, increased egg deposition sometimes occurs in the border rows, resulting in a source of heterogeneity. It was not known at the outset of these experiments whether *P. maculipennis* possessed this habit; accordingly, in 1958, the plots were subdivided (see preceding section) so as to allow comparison of populations between interior and exterior strata. Analysis of population differences by Student's T test revealed no evidence of "border effect" in counts of any of the immature stages of the moth. Since the plots were almost square in shape, directional distribution (Ullyett, 1947) was not a factor in the present experiments.

*Sampling Intervals*

Proper timing is extremely important when sampling a multivoltine species, due to the tendency of stages of the same generation to overlap in the field. Collection of the insect itself for this purpose was too time-consuming to warrant serious consideration in the present study. Accordingly, the stage of development was determined by two methods:

1. The insect was reared continuously during the season in an outdoor study cage (Harcourt, 1957a) adjacent to the experimental plots. Environmental conditions in the cage were not appreciably different from those in the study plots, and consequently the rate of development in the cage closely paralleled that in the field.

2. At least once daily, the mean temperature during the previous 24 hours was examined in relation to velocity of development curves for the various stages (Harcourt, 1954). It was thus possible to judge with a high degree of accuracy the existing stage of development.

Estimates of population density were obtained for each of five age intervals, namely, egg, larva, Periods 1-3, and pupa. Because the life cycle of *P. maculipennis* is very short, there was a rapid day-to-day decline in populations, particularly during the period of larval activity. Consequently, it was necessary to complete assessments of population of certain age intervals within a few hours of the same day. The calendar dates of sampling, even with corresponding generations, varied widely from year to year.

*Egg.*—The time of sampling for this stage was dependent upon the completion of oviposition. The female moths begin to oviposit on the day of emergence. Egg-laying lasts about 10 days, the peak occurring on the first night of oviposition except when sunset temperatures are below 66°F. Most of the eggs are laid on the upper leaf epidermis, singly, or in groups of two to eight. The eggs are very small (.44 × .26 mm.), but can be readily counted in the field with a low-powered hand lens. Egg populations were estimated by direct sampling; in addition, substantial numbers were collected and reared in the laboratory to determine viability. There was no evidence of parasitism during this stage.

*Larva.*—The newly hatched larvae wander for a short distance in search of suitable leaf tissues in which to construct mines, there being a limited amount of plant-to-plant dispersal in response to crowding. Populations of first-instar larvae in mines are extremely stable. The minute mines are difficult to find, and

population estimation during the first instar was considered too time-consuming and inaccurate to be profitable. Although larvae of the remaining instars are surface feeders, they sometimes feed with head and thorax buried in the leaf.

Mortality factors during the larval stage were assessed by subdividing the larval interval. The interval was divided into three periods, corresponding to periods when certain parasites killed the host. Populations of larvae in Period 1 and at the beginning of Periods 2 and 3 were estimated by direct sampling, and the mortality caused by parasites, by collecting host larvae and rearing them in the laboratory.

Period 1: From hatching to middle of fourth instar. In this period, no mortality was caused by parasites. The larvae are small, and, because of their feeding habits, well concealed from birds and mammalian predators. Arthropod predators were, for the most part, unimportant. Rainfall caused considerable mortality during this period. The larvae are readily disturbed by rainfall, and are washed, or wriggle, into leaf axils where they quickly drown in water trapped therein. Some spin threads and drop to the ground where they perish in pockets of water in the soil. To determine the effects of a given rainfall, it was necessary to sample populations within a few hours of its termination.

Period 2: From middle of fourth instar to cocoon formation. The parasite *Microplitis plutellae* (Mues.) kills the host larva and emerges during this period.

Period 3: From cocoon formation to pupation. The parasite *Horogenes insularis* (Cress.) kills the host larva and emerges during this period (Harcourt, 1960a).

The number of individuals destroyed by parasites in Periods 2 and 3 was determined by rearing larvae collected at the time of sampling. This provided the rate of parasitism at the *beginning* of each period. Strictly speaking, it was a potential, rather than actual value because both parasitized and unparasitized larvae were subject to mortality from other factors during the *remainder of the period*. However, differences between potential and actual mortalities were limited in magnitude by the extremely short duration of Periods 2 and 3.

*Pupa.*—Pupae in cocoons were easily detected and populations could be readily estimated by direct population sampling. However, examination of empty cocoons could not be used as a clue to activity of the parasite *Diadromus plutellae* (Vier.). The cocoons, which are extremely well attached to the plant, accumulate from generation to generation, and it is impossible to judge the age of a cocoon with any degree of accuracy. Accordingly, pupae were collected at the time of sampling and brought to the laboratory for rearing and dissection. Evidence of mortality due to arthropod and mammalian predators was not observed. Predation by birds[1] was evident only in the fall of the year.

## Statistical Analysis

### *Scope of the Study*

Although complete life tables were constructed for 14 successive generations during 1958 to 1960, in only four of those generations (Tables I-V) were the data recorded in such a way as to permit detailed study of the variation between samples. During the remaining generations, sample units were selected at random, and sampling was continued until the mean number of individuals per quadrant possessed acceptable error limits.

[1]Chiefly, the brown-headed cowbird, *Molothrus ater* (Boddaert), the song sparrow, *Melospiza melodia* (Wilson), and the redwing, *Agelaius phoeniceus* (Linn.).

TABLE I
Analysis of variance of egg counts of the third generation of *P. maculipennis*, 1960 (Table III)

| Source of variation | Expected mean square[1] | d.f. | Observed mean square | F |
|---|---|---|---|---|
| Between plants | | | | |
| Blocks | $\sigma^2_s + 4\sigma^2_p + 64\sigma^2_b$ | 3 | 0.18 | 0.95 |
| Plants within blocks | $\sigma^2_s + 4\sigma^2_p$ | 60 | 0.19 | 1.73[2] |
| Within plants | | | | |
| Quadrants | $\sigma^2_s + 64\sigma^2_q$ | 3 | 0.11 | 1.00 |
| Residual | $\sigma^2_s$ | 189 | 0.11 | |

[1]$\sigma^2_s$, $\sigma^2_p$, etc., are population parameters; $s^2_s$, $s^2_p$, in the text are estimates of these parameters.
[2]Significant at the one per cent level.

*Statistical Methods*

All the counts were assessed by analysis of variance. To ensure the validity of this method, the data were transformed using the logarithm of $(x + 1)$, where $x$ is equal to the observed count (Harcourt, 1960b). However, because of practical disadvantages attending the use of logarithms in the presentation of life table data, the population means in the present study were expressed in terms of the original variates (Table III). All the other parameters were based on the transformed population. The analysis of variance is illustrated in Table I using one of the sets of data.

All the numerical differences that follow were statistically significant unless otherwise stated.

**Sources of Variation**

Differences between blocks occurred in 1960 in numbers of larvae, Period 1 (2nd sampling, 3rd generation), and of larvae, Period 3 (parasitized by *H. insularis*, 3rd, 4th generations). Differences between plants occurred in all age intervals except larvae, Period 1 (2nd sampling, 3rd generation) in 1960. Differences between quadrants occurred in numbers of eggs of the 1958 generation, and in numbers of larvae, Period 1 (2nd sampling, 2nd generation) and larvae, Period 3 (parasitized by *H. insularis*, 2nd, 3rd generations) in 1960. The analysis of variance thus indicated that only plant-to-plant variation need be taken into account in sampling of *P. maculipennis*.

The fact that variation between plants constitutes the major source of population variation is of considerable interest in that this principle has not been previously demonstrated for an insect pest of a field crop. Predominant inter-tree variation has been shown to characterize natural populations of a number of forest and orchard species (Morris, 1955; Stark, 1952; Prebble, 1943; Morris and Reeks, 1954; LeRoux and Reimer, 1959), indicating that the principle may well apply to insect defoliators in general.

**Components of Variance**

After it was known which factors contributed significantly to the overall variation, the magnitudes of the individual contributions were estimated. In this study, estimates of the intra-plant ($S^2_s$) and inter-plant ($S^2_p$) error variances were calculated and used to determine the optimum number of quadrants per plant and also the number of plants required to obtain an estimate of population density with a specified standard error.

TABLE II

Significance of variation due to blocks, plants, and quadrants, in samples of the immature stages of four generations of *P. maculipennis* on cabbage[1], Merivale, Ont.

| Age interval | Blocks | Plants | Quadrants |
|---|---|---|---|
| *Generation 2, 1958* | | | |
| Egg | —[2] | xx[3] | x[4] |
| Larva | | | |
| Period 1 | | | |
| 1st sampling | — | xx | — |
| 2nd sampling | — | xx | — |
| Period 2 | — | xx | — |
| Period 3 | — | xx | — |
| Pupa | — | xx | — |
| *Generation 2, 1960* | | | |
| Egg | — | xx | — |
| Larva | | | |
| Period 1 | | | |
| 1st sampling | — | xx | — |
| 2nd sampling | — | xx | xx |
| 3rd sampling | — | xx | — |
| Period 2 | — | xx | — |
| Period 3 | | | |
| Total | — | xx | — |
| Parasitized by *H. insularis* | — | xx | — |
| Pupa | | | |
| Total | — | xx | — |
| Parasitized by *D. plutellae* | — | xx | — |
| *Generation 3, 1960* | | | |
| Egg | — | xx | — |
| Larva | | | |
| Period 1 | | | |
| 1st sampling | — | xx | — |
| 2nd sampling | xx | — | — |
| 3rd sampling | — | xx | — |
| Period 2 | — | xx | — |
| Period 3 | | | |
| Total | — | xx | — |
| Parasitized by *H. insularis* | x | xx | x |
| Pupa | | | |
| Total | — | xx | — |
| Parasitized by *D. plutellae* | — | xx | — |
| *Generation 4, 1960* | | | |
| Egg | — | xx | — |
| Larva | | | |
| Period 1 | | | |
| 1st sampling | — | xx | — |
| 2nd sampling | — | xx | — |
| Period 2 | — | xx | — |
| Period 3 | | | |
| Total | — | xx | — |
| Parasitized by *H. insularis* | x | xx | x |
| Pupa | | | |
| Total | — | xx | — |
| Parasitized by *D. plutellae* | — | xx | — |

[1]64 plants per sample
[2]Not significant
[3]Significant at the 1 per cent level
[4]Significant at the 5 per cent level

TABLE III

Estimates of mean densities and of variance components in samples of the immature stages of four generations of *P. maculipennis*, the foliage being taken from each of four quadrants from each of 64 cabbage plants, Merivale, Ont.

| Age interval | Mean number per quadrant, $\bar{x}$ | Variance component[2] | |
|---|---|---|---|
| | | Within plants, $S^2_s$ | Between plants, $S^2_p$ |
| *Generation 2, 1958* | | | |
| Egg | 8.85±1.4[1] | 0.20 | 0.04 |
| Larva | | | |
| Period 1 | | | |
| 1st sampling | 8.31± .64 | 0.08 | 0.02 |
| 2nd sampling | 3.73± .32 | 0.05 | 0.02 |
| Period 2 | 3.29± .31 | 0.04 | 0.03 |
| Period 3 | 2.77± .24 | 0.06 | 0.01 |
| Pupa | 1.14± .10 | 0.06 | 0.01 |
| *Generation 2, 1960* | | | |
| Egg | 4.08± .63 | 0.10 | 0.02 |
| Larva | | | |
| Period 1 | | | |
| 1st sampling | 1.75± .23 | 0.06 | 0.06 |
| 2nd sampling | 1.85± .18 | 0.05 | 0.02 |
| 3rd sampling | 1.63± .15 | 0.08 | 0.03 |
| Period 2 | 1.63± .15 | 0.08 | 0.04 |
| Period 3 | | | |
| Total | 1.58± .11 | 0.03 | 0.01 |
| Parasitized by *H. insularis* | 0.15± .04 | 0.03 | 0.01 |
| Pupa | | | |
| Total | 1.43± .13 | 0.05 | 0.02 |
| Parasitized by *D. plutellae* | 0.16± .04 | 0.05 | 0.01 |
| *Generation 3, 1960* | | | |
| Egg | 12.08± .56 | 0.11 | 0.02 |
| Larva | | | |
| Period 1 | | | |
| 1st sampling | 11.97+1.1 | 0.06 | 0.03 |
| 2nd sampling | 11.37± .80 | 0.17 | 0.00 |
| 3rd sampling | 5.98± .24 | 0.03 | 0.03 |
| Period 2 | 5.38± .26 | 0.04 | 0.02 |
| Period 3 | | | |
| Total | 3.68± .15 | 0.05 | 0.01 |
| Parasitized by *H. insularis* | 0.82± .12 | 0.05 | 0.03 |
| Pupa | | | |
| Total | 2.87± .14 | 0.05 | 0.04 |
| Parasitized by *D. plutellae* | 0.28± .07 | 0.05 | 0.01 |
| *Generation 4, 1960* | | | |
| Egg | 14.97±2.7 | 0.10 | 0.02 |
| Larva | | | |
| Period 1 | | | |
| 1st sampling | 4.29± .41 | 0.05 | 0.03 |
| 2nd sampling | 3.92± .39 | 0.05 | 0.03 |
| Period 2 | 4.42± .38 | 0.05 | 0.02 |
| Period 3 | | | |
| Total | 3.76± .25 | 0.06 | 0.02 |
| Parasitized by *H. insularis* | 1.45± .18 | 1.10 | 0.02 |
| Pupa | | | |
| Total | 2.31± .15 | 0.06 | 0.02 |
| Parasitized by *D. plutellae* | 0.39± .05 | 0.05 | 0.01 |

[1]Standard error.
[2]Transformed [log (x+1)].

TABLE IV
Estimation of numbers of quadrants per plant required to minimize cost of sampling for immature stages of *P. maculipennis*

| Age interval | (1) Mean ratio of variance components $S^2_s/S^2_p$ | (2) Cost ratio $C_p/C_s$ | Number of samples $n=\sqrt{1 \times 2}$ |
|---|---|---|---|
| Egg | 5.2 | .11 | .76 |
| Larva, Period 1 | 2.1 | .14 | .54 |
| Larva, Period 2 | 1.9 | .14 | .52 |
| Larva, Period 3 | 3.8 | .12 | .67 |
| Pupa | 4.0 | .12 | .69 |

The inter-plant variance was obtained from the mean square for plants and the residual mean square by the formula (MSP — MSR) ÷ 4. For example, from the mean squares in Table I, $S^2_p = (.19 - .11) \div 4 = .02$, and $S^2_s = .11$. These components of variance are listed in Table III.

### Mean Density

Estimates of population densities of *P. maculipennis* and of the effects of some mortality factors are listed in Table III. Each mean was based on examination of the foliage from each of four quadrants from each of 64 plants. Standard errors were computed by the formula $S_{\bar{x}} = S/\sqrt{64}$.

Table III shows that the standard error was usually 10 per cent of the mean or less. An exception may be noted in the mean density for eggs of the 1958 generation. Exceptions also occurred in 1960 in the mean density for eggs, (2nd, 4th generations), larvae, Period 1 (1st sampling, 2nd generation), larvae, Period 3 (parasitized by *H. insularis*), where the standard error ranged from 12 to 27 per cent, and pupae (parasitized by *D. plutellae*), where the standard error ranged from 13 to 25 per cent.

### Optimum Allocation of Sampling Resources

*Specified Precision*

To be meaningful, life tables should incorporate a wide variety of crop conditions. However, the value of such a study may be reduced by setting such a high degree of sampling precision[2] that the number of conditions is limited, particularly at endemic levels of population. At the same time, it is useless to secure data of doubtful statistical significance over a wide range of crop conditions. As a suitable compromise between the two extremes, a 10 per cent standard error was adopted in the present study. This degree of precision has been found satisfactory in life table studies on certain forest and orchard insects (Morris, 1955; Stark, 1959; LeRoux and Reimer, 1959).

*Number of Quadrants per Plant*

Decision as to the optimum number of sample units (quadrants) to draw per plant was based on the relationship between the intra- and inter-plant variance components (Table III) and the cost of moving from plant to plant. The optimum number, $n$, is derived from the formula, $n = \sqrt{(S_s^2/S_p^2)(C_p/C_s)}$ where $C_p$ is the cost of moving from one plant to another, and $C_s$ is the cost of examining one quadrant.

Table IV summarizes the calculations leading to $n$. The ratios of the variance components for each age interval were averaged for all samplings,

[2]*Precision* is used in the sense defined by Finney (1953) and concerns the reproducibility of an estimate.

including those taken to determine the effects of secondary variables (i.e., parasites).

It required 0.5 man-minutes to locate a new sample plant and to prepare for sampling. The number of man-minutes required to dissect and examine a single quadrant for the various intervals was estimated as follows: Egg, 4.5; Larva, Period 1, 3.5; Larva, Period 2, 3.5; Larva, Period 3, 4.0; Pupa, 4.0. On the basis of the values for $n$ it is recommended that not more than one quadrant per plant be examined for all stages. Choice of quadrants should, of course, be by random selection from each plant.

*Number of Plants to Sample for a 10 Per Cent Error*

To estimate the number of plants required for a 10 per cent standard error, it was first necessary to obtain the coefficients of inter-plant variation. These coefficients, based on a single quadrant per plant, were calculated from the components of variance (Table III) and the means (expressed as logarithms) as follows:

$$\text{C.V.} = \frac{100}{\bar{x}} \sqrt{S_s^2 + S_p^2}$$

For example, for numbers of eggs in generation 3, 1960:

$$\text{C.V.} = \frac{100}{.991} \sqrt{.11 + .02} = 37\%$$

The number of plants required is derived from the coefficient of inter-plant variation as $n_p = (\text{C.V.}/10)^2$. Thus, for a 10 per cent error in mean number of eggs in generation 3, a total of $(37/10)^2$, or 14, plants should be sampled, taking one quadrant per plant. The coefficients of inter-plant variation and numbers of plants required are listed in Table V.

**Suggested Sampling Plan**

The suggested sampling plan (Table VI) is obtained from Table V by averaging the number of plants required for each age interval and rounding upwards to a multiple of 10. The plan does not take into account secondary variables such as larvae parasitized by *H. insularis* and pupae parasitized by *D. plutellae*. However, the policy of taking a sample large enough for the most important variables and accepting whatever precision is obtained for the less important ones has been endorsed by other workers (Hanson *et al.*, 1953; LeRoux and Reimer, 1959).

The sampling plan should provide a reasonable degree of precision for life table studies of *P.maculipennis*. At the levels of population encountered in the present study, the plan would provide for a 10 per cent standard error in all but a very few samplings. Exceptions are to be noted in 1960 in per cent standard error for eggs (4th generation) 12, larvae, Period 1, (2nd generation, 1st sampling), 15, and pupae (total, 2nd generation), 12.

The amount of sampling required for a standard error of 10 per cent would vary with the population density. At endemic levels of population many more samples would be needed to obtain this precision. Conversely, fewer samples would be needed at epidemic levels. This characteristic appears to be inherent with population distributions of the negative binomial type (Morris, 1955; LeRoux and Reimer, 1959).

**Summary**

Variation between samples of immature stages of the diamondback moth, and between some of the mortality factors affecting its abundance, on cabbage, were determined in long-term study plots at Merivale, Ontario. For each of five

TABLE V
Estimation of numbers of plants to be sampled for a 10 per cent error, on the basis of single quadrant samples, for immature stages of *P. maculipennis*

| Age interval | Coefficient of variation | Number of plants required |
|---|---|---|
| Egg | | |
| Generation 2, 1958 | 123 | 151 |
| Generation 2, 1960 | 122 | 149 |
| Generation 3, 1960 | 37 | 14 |
| Generation 4, 1960 | 142 | 201 |
| Larva, Period 1 | | |
| Generation 2, 1958, 1st sampling | 62 | 38 |
| 2nd sampling | 69 | 48 |
| Generation 2, 1960, 1st sampling | 107 | 114 |
| 2nd sampling | 77 | 59 |
| 3rd sampling | 73 | 53 |
| Generation 3, 1960, 1st sampling | 76 | 58 |
| 2nd sampling | 56 | 31 |
| 3rd sampling | 32 | 10 |
| Generation 4, 1960, 1st sampling | 76 | 58 |
| 2 nd sampling | 80 | 64 |
| Larva, Period 2 | | |
| Generation 2, 1958 | 75 | 56 |
| Generation 2, 1960 | 75 | 56 |
| Generation 3, 1960 | 38 | 14 |
| Generation 4, 1960 | 69 | 48 |
| Larva, Period 3 | | |
| Total | | |
| Generation 2, 1958 | 68 | 46 |
| Generation 2, 1960 | 55 | 30 |
| Generation 3, 1960 | 33 | 10 |
| Generation 4, 1960 | 54 | 29 |
| Parasitized by *H. insularis* | | |
| Generation 2, 1960 | 241 | 581 |
| Generation 3, 1960 | 112 | 125 |
| Generation 4, 1960 | 98 | 96 |
| Pupa | | |
| Total | | |
| Generation 2, 1958 | 72 | 52 |
| Generation 2, 1960 | 74 | 55 |
| Generation 3, 1960 | 39 | 15 |
| Generation 4, 1960 | 51 | 26 |
| Parasitized by *D. plutellae* | | |
| Generation 2, 1960 | 225 | 506 |
| Generation 3, 1960 | 189 | 357 |
| Generation 4, 1960 | 110 | 121 |

TABLE VI
Suggested sampling plan for life-table studies on *P. maculipennis*

| Age interval | Number of quadrants per plant | Number of plants |
|---|---|---|
| Egg | 1 | 150 |
| Larva | | |
| Period 1 | 1 | 50 |
| Period 2 | 1 | 50 |
| Period 3 | 1 | 40 |
| Pupa | 1 | 40 |

age intervals (egg; larva, Period 1; larva, Period 2; larva, Period 3; and pupa), inter-plant variance was the major source of population variance. Intra-plant and block differences were rarely significant. The most appropriate sample unit was the crown quadrant. Application of the variance component technique indicated that not more than one sample unit per plant should be taken for each age interval. To estimate population means within a 10 per cent standard error, it is recommended that 150, 50, 50, 40, and 40 plants, respectively, be sampled for the five age intervals.

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**References**

Finney, D. J. 1953. An introduction to statistical science in agriculture. J. Wiley and Sons Inc., New York.

Hansen, M. H., W. N. Hurwitz, and W. G. Madow. 1953. Sample survey methods and theory. Vol. 1. Methods and applications. J. Wiley and Sons Inc., New York.

Harcourt, D. G. 1954. The biology and ecology of the diamondback moth, *Plutella maculipennis* (Curt.), in eastern Ontario. Ph.D. Thesis. Cornell University.

Harcourt, D. G. 1957a. An outdoor study cage for phytophagous insects. *Ann. Rept. Ent. Soc. Ontario* 87: 11-14.

Harcourt, D. G. 1957b. Biology of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera : Plutellidae), in eastern Ontario. II. Life history, behaviour, and host relationships. *Canadian Ent.* 89: 554-564.

Harcourt, D. G. 1960a. Biology of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera : Plutellidae), in eastern Ontario. III. Natural enemies. *Canadian Ent.* 92: 419-428.

Harcourt, D. G. 1960b. Distribution of the immature stages of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera : Plutellidae), on cabbage. *Canadian Ent.* 92: 517-521.

LeRoux, E. J. and C. Reimer. 1959. Variation between samples of immature stages, and of mortalities from some factors, of the eye-spotted bud moth, *Spilonota ocellana* (D. & S.) (Lepidoptera : Olethreutidae), and the pistol case-bearer, *Coleophora serratella* (L.) (Lepidoptera : Coleophoridae), on apple in Quebec. *Canadian Ent.* 91: 428-449.

MacNay, C. G. 1959. Summary of important insect infestations, occurrences and damage in Canada in 1958. *Ann. Rept. Ent. Soc. Ontario* 89: 73-87.

Morris, R. F. 1955. The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. *Canadian J. Zool.* 33: 225-294.

Morris, R. F. and C. A. Miller. 1954. The development of life tables for the spruce budworm. *Canadian J. Zool.* 32: 283-301.

Morris, R. F., C. A. Miller, D. O. Greenbank, and D. G. Mott. 1958. The population dynamics of the spruce budworm in Eastern Canada. *Proc. Xth Intern. Congr. Ent.* 4: 137-149.

Morris, R. F. and W. A. Reeks. 1954. A larval population technique for the winter moth, *Operophtera brumata* (Linn.) (Lepidoptera : Geometridae). *Canadian Ent.* 86: 433-438.

Prebble, M. L. 1943. Sampling methods in population studies of the European spruce sawfly, *Gilpinia hercyniae* (Hartig), in eastern Canada. *Trans. Roy. Soc. Canada* 37: 93-126.

Stark, R. W. 1952. Analysis of a population sampling method for the lodgepole needle miner in Canadian Rocky Mountain Parks. *Canadian Ent.* 84: 316-321.

Stark, R. W. 1959. Population dynamics of the lodgepole needle miner, *Recurvaria starki* Freeman, in Canadian Rocky Mountain Parks. *Canadian J. Zool.* 37: 917-943.

Ullyett, G. C. 1947. Mortality factors in populations of *Plutella maculipennis* Curtis (Tineidae : Lep.), and their relation to the problem of control. *South Africa Dept. Agr. and Forestry Ent. Mem.* 2: 77-202.

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## Book Review

**Evolution: Process and Product,** by Edward O. Dodson. Revised edition of *A Textbook of Evolution.* Reinhold Publishing Corporation, New York; Chapman and Hall, Ltd., London; June 15, 1960. pp. xvi + 352, 113 Figs. College Edition, $5.75; Trade Edition, $6.90.

Professor Dodson states that his aim in writing his earlier book and in preparing the present revised edition is to make available to students the large quantity of modern information and theory on evolution. In my opinion he has succeeded well in this purpose. He gives a comprehensive, intelligible, and balanced account. In a work of this kind it is of course impossible to do more than present broad outlines, with a selection of illustrative detail. However, in the chapters closest to my interests the main theories have been covered, in simple but in general in fair and informative summary. Each chapter is followed by a list of references which, although brief, is well suited to guiding the interested student farther into the literature.

Professor Dodson begins with a chapter on Darwin's concept of evolution. Then come four chapters on evidences of evolution; these contain interesting examples, both modern and classical. Two brief and over-simplified chapters on history of evolutionary thought and on main problems of evolution follow, concluding Part One. Part Two is a descriptive account of the phylogeny of the living world including theories of the origin of life. Part Three deals with the genetic basis of variation. Part Four deals with the origin and distribution of species, touching on selection, adaptation and its manifestations, population genetics, species formation, chromosome changes, and biogeography. Part Five deals with theories of man's evolutionary future.

This book contains little in the way of new ideas or synthesis, but it is packed with information presented in logical sequence and in plain English. Purists may find the didactic style more reminiscent of a high school book than of a university text, but few university texts contain so much or give such a useful entree to key literature. The poorest feature of the book is the illustrations. Most of these are necessarily borrowed, but many have suffered in the process; the halftones in particular are coarse and unsatisfactory.

Professor Dodson's book will be invaluable to the students for whom it is designed. In my opinion it can also be read with profit by biologists and by educated non-biologists at a wide variety of levels of interest.

EUGENE MUNROE

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## Election of Officers of the Entomological Society of Canada

As a result of the recent balloting, the following members have been elected:

President-elect, 1961-62 ..... C. W. FARSTAD

Directors-at-large, 1961-63 ..... R. S. BIGELOW, M. D. PROVERBS, E. J. LEROUX

Directors representing regional entomological societies, 1961-63 ..... J. A. DOYLE, R. J. HERON, R. W. SALT

L. L. REED, *Secretary.*

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